Assessing the availability of pollinator foraging resources using remote sensing technology

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Abstract

Nectar sugar is the primary energy source for pollinators and an integral part of their diet. The supply of nectar sugar available to pollinators has been quantified at habitat and landscape scales, but few studies have explored how nectar sugar varies within habitat types, at finer scales. This thesis quantifies fine-scale variability in nectar supply in linear habitat features managed for pollinator conservation at a UK arable farm, and explores for the first time whether this variability can accurately be measured using remote sensing.

In a study of sown and naturally regenerated field margins, I find substantial variation between margin types and individual margins in the quantity of nectar sugar supplied (mg/m^2/day), and a significant positive relationship between nectar sugar supply and honeybee abundance.

Baseline assessment of the spatial and temporal distribution of nectar sugar across a farmed landscape is necessary to identify gaps in supply and inform pollinator conservation strategies. Such assessment must include variability within habitat types demonstrated in this thesis. Traditional ground-based quadrat surveys are time consuming, resource-intensive and require expertise. An alternative is to use remotely-sensed imagery to classify nectar-rich flowering plant species. I demonstrate high overall accuracies (92.3%-98.7%) and variable user's and producer's accuracies for 11 nectar-rich flowering plant species, using multispectral imagery (spatial resolution 3-7cm) obtained via manned aircraft and unmanned aerial vehicle platforms. I also demonstrate that two of the major nectar producers, *Centaurea nigra* and *Cirsium arvense*, are more accurately classified when combined as a single category (Thist$_{group}$) and that area classified as Thist$_{group}$ is correlated with the mean number of floral units on the ground (units/m^2).

The methods developed in this thesis have multiple applications for pollinator conservation in agricultural settings, providing they are scaleable. The final Chapter discusses these possible applications and next steps for research.

Table of Contents

List of Figures

List of Tables

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Author Contributions

I am the lead author on each Chapter in this thesis and performed the majority of preparation, fieldwork and analysis with both external and internal collaboration. My supervisors Dr Lynn V. Dicks and Professor Andrew A. Lovett helped to conceive the ideas, reviewed and edited each Chapter and their corresponding manuscripts and are authors on each manuscript.

Chapter 2 I carried out the preparation, fieldwork (ground-truth remote-sensing surveys) and analysis for this Chapter. Spectrum aviation acquired the aerial imagery and carried out the pre-processing. I drafted the Chapter and paper manuscript. Lynn V. Dicks and Andrew A. Lovett reviewed both Chapter and manuscript. Andrew A. Lovett provided advice on the use of GIS and remote-sensing platforms.

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Chapter 3 I prepared and drafted this Chapter and carried out the fieldwork (floral surveys / bee surveys) and analysis. Lynn V. Dicks provided fieldwork advice and support and reviewed this Chapter. Andrew A. Lovett reviewed this Chapter. Chapter 3 is being combined with Chapter 4 into a single manuscript which is currently in preparation.

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Chapter 1

Introduction: The importance of managing floral resources for pollinators in farmed landscapes

Contributing to the pollination of approximately 88% of flowering plants globally (Ollerton et al., 2011), including 75% of crops upon which humanity depends (Klein et al., 2007), pollinators are integral to the provision of multiple ecosystem services. These range from increased crop yield to the provision of aesthetically-pleasing landscapes (Akbar et al., 2003; Klein et al., 2007). The trends for many species are not known (Goulson et al., 2015; Ollerton, 2017) and yet significant declines have been found for others (e.g. Bartomeus et al., 2013; Goulson, 2010; Powney et al., 2019). I start this Chapter by reviewing in Section 1.1, the status and significance of pollinators, followed by the multiple threats that they face.

One of the predominant drivers of pollinator decline is agricultural intensification (Goulson et al., 2015; Potts et al., 2016), which typically leads to resource-poor landscapes. However, as I review in Section 1.2, numerous studies have demonstrated that increasing floral resources within arable landscapes can to an extent reverse the loss of floral resources and increase pollinator richness and abundance (Albrecht et al., 2021; Lowe et al., 2021; Zamorano et al., 2020). In Section 1.3, I consider the importance of both nectar and pollen in the pollinator diet. In particular, I choose to focus on nectar sugar in this PhD and its availability to pollinators. This is due to its essential role as the key pollinator energy source, needed to fuel foraging flight so that remaining nutritional needs can be met (Wilmer, 2011). Other studies have also chosen to quantify the national (Baude et al., 2016) and landscape-level (Langlois et al. 2020; Timberlake et al., 2019; Timberlake et al., 2021) nectar sugar provision available to pollinators. Each of these studies consider the differences in nectar sugar provision between individual habitats, but do not consider the fine-scale nectar sugar variability within different habitat types (exceptions are Hicks et al., 2016 and Holl et al., 1995). The first aim of my PhD is to therefore focus on the nectar sugar supply (mg/m^2/day) across arable field margins and to relate this to bee abundance.

In Section 1.5, I look at the importance of assessing the spatial and temporal distributions of floral resources across an agricultural landscape. These need to take into account the different life-histories, phenological patterns and foraging distances of pollinators (Greenleaf et al., 2007; Jachuła, 2021; Timberlake et al., 2019). Surveys of floral abundance/ cover, from which floral resources such as nectar sugar are estimated, traditionally consist of ground-based quadrat surveys (e.g. Baude et al., 2016; Hicks et al., 2016; Jachuła, 2021; Timberlake et al., 2019). These can be time-consuming and only ever provide an estimate rather than the true distribution of floral resources (Barnas et al., 2019; Willcox et al., 2018).

One potential alternative is to take advantage of the rapidly-developing remote-sensing technologies that are now available and which are a high enough resolution to map the floral component of individual flowering plant species (e.g. Carl et al., 2017; de Sá et al., 2018; Horton et al., 2017). The second aim of my PhD, is to ask whether nectar-rich flowering plant species can be classified using high-resolution (3-7cm) multispectral imagery. In Section 1.6 of this Chapter, I therefore consider the advantages of remote-sensing techniques relative to ground-based surveys and in Section 1.7, I focus on the basic principles of remote-sensing. In Section 1.8, I consider the application of remote-sensing technologies for quantifying pollinator resources. Finally, in Section 1.9 I outline my thesis aims and structure.

1.1 Pollinators: their global significance and threats

Pollinators encompass a diverse range of taxa globally, many species of which are not yet known (Ollerton, 2017). Quantifying the total number of pollinating species according to taxa is therefore difficult, but includes many Lepidoptera, Coleoptera, Diptera and Hymenoptera, the latter order containing an approximate 22000 bee species (Goulson et al., 2015). Infrequent flower visitors from many other orders may also play a part in pollination (Wardhaugh, 2015). The Lepidoptera is the most species-rich order, containing greater than 140,000 potential flower-visiting species (Ollerton, 2017).

Combined, this global pollinator community is essential for maintaining many flowering plant communities across the world (Goulson et al., 2008; Ollerton et al., 2011; Potts et al., 2016). Ollerton et al. (2011) calculated that the global percentage of flowering plant species that are pollinated by animals is 87.5%, while Rodger et al. (2021) suggest that in the absence of pollinators, approximately one third of flowering plant species would set no seed at all. The plant communities that rely upon pollinators themselves provide enormous benefits to humanity, whether due to their aesthetic value (e.g. Akbar et al., 2003; Clay and Daniel, 2000), use as existing or future food sources (Klein et al., 2007; Ulian et al., 2020) or, the fact that they in turn support pollinators and other species groups that provide additional ecosystem functions such as pest control (Klein et al., 2007; Sivinski et al., 2011).

Population trends for many pollinators around the world remain unknown (Goulson et al., 2015) and, establishing suitable pollinator monitoring programmes could go a long way towards addressing knowledge gaps (Woodard et al., 2020). However, significant declines have been documented for some species groups and regions (e.g. see Goulson et al., 2008; Goulson et al., 2015; Grixti et al., 2009; Ollerton, 2017; Potts et al., 2016; Powney et al., 2019; Warren et al., 2021). It is well-established for example, that Europe has experienced declines in many species of bumblebee (Goulson, 2010; Goulson et al., 2005; Goulson et al., 2008; Kosior et al., 2007). Research focusing on the North American continent has also demonstrated declines in *Bombus*, both in terms of species richness (Bartomeus et al., 2013; Grixti et al., 2009) and in terms of the distribution of certain species such as *B. pensylvanicus* (Grixti et al., 2009). Bias in the pollinator literature towards *Bombus* species (in addition to *Apis* species) has been recognised (Millard et al., 2020), although declines are not restricted to bumblebees alone. Powney et al. (2019) for example, found declines in 33% of 353 British wild pollinating species, although 10% had also increased in the same timeframe (1980-2013). Since 1990, declines have been found in six out of 17 European grassland butterfly species (vanSway et al., 2019).

A geographical pollinator research bias towards North America and Europe was also identified by Millard et al. (2020). However, as noted by the authors, text-analysis methods can themselves be subject to bias, for example due to the exclusion of non-

English studies (Millard et al., 2020). Of the studies that do exist in other regions of the world, pollinator decline is also evident (Ollerton, 2017).

The threats contributing to pollinator decline the world over are complex and can exert pressures upon pollinators individually as well as interactively (González-Varo et al., 2013; Goulson et al., 2015; LeBuhn and Vargas Luna, 2021; Siviter et al., 2021; Vanbergen et al., 2021). Threats include the loss of suitable habitat that provides adequate floral and nesting resources, crop management practices including the use of pesticides, the presence of pollutants in forage plants, the introduction of invasive plant species and, the introduction of non-native pollinator species and their associated new parasites or competitive interactions (Dicks et al., 2021; González-Varo et al., 2013; Goulson et al., 2015; LeBuhn and Vargas Luna, 2021; Potts et al., 2010; Tonietto and Larkin, 2018). Using a Delphi process to draw upon pollinator expert knowledge, Dicks et al. (2021) identified land cover type/structure as well as land management practices as being the two most important drivers of decline for pollinators around the world and, the drivers for which there is the most evidence. However, other factors also build up layers of pressures upon pollinator communities that can influence their long-term survivability (LeBuhn and Vargas Luna, 2021).

Pressures upon pollinators such as those resulting from the intensification of agricultural practices, have been shown to work synergistically. For example, exposure to complex mixes of chemicals in intensively-managed agricultural environments increases bee mortality (Siviter et al., 2021; Vanbergen et al., 2021). Pressures have also been shown to work additively, such as the interaction between nutrition and agrochemicals upon bee mortality, whose combined effects are equal to the sum of the effects of the two pressures individually (Siviter et al., 2021; Vanbergen et al., 2021). However, the majority of studies investigating the interactive effects of pressures upon bees focus on *Apis mellifera.* This highlights the need for further research in alternative taxa, especially because the research that does exist indicates that the relationship between interacting pressures and bee mortality varies according to taxon (Siviter et al., 2021; Vanbergen et al., 2021). The pressures exerted by individual drivers also vary by taxa. Gradish et al. (2018) for example, argue that pesticide risk assessments should take into account potential exposure routes of different species. Ground-nesting *Bombus* species for example, are likely to have greater exposure to pesticide residue through their nesting habits, than species that do not nest in the ground (Gradish et al., 2018).

A changing climate poses an increasing threat to pollinator communities (Dicks et al., 2021; Goulson et al., 2015; Kammerer et al., 2021). Dicks et al. (2021) note the uncertainty surrounding the relative importance of climate change when compared to other contributors to pollinator decline. However, research as to the effects of climate change upon pollinators is expanding rapidly, with Kammerer et al. (2021) demonstrating that climatic variables such as temperature and rainfall are key predictors of abundance and richness of wild bees in the north-eastern United States, more so than landscape-related variables such as landscape quality. Soroye et al. (2020) found 17% and 46% declines in the probability of bumblebee species occupancy within 100km X 100km quadrats for Europe and North America respectively, linked to changes in precipitation and temperature as a result of climate change. A review by Vasiliev and Greenwood (2021) suggested that the effects of a changing climate upon pollinator communities are frequently underestimated and that climate change is likely leading to the loss of heterogeneity at the community, genetic and species levels. Some impacts of climate change upon pollinator communities are likely not yet apparent. An earlier study by Bartomeus et al. (2011) for example, suggested that divergences in phenological patterns between bees and the plants that they visit had not yet happened, as rising temperatures led to concurrent phenological advances in plants and bees. However, the authors also noted that these divergences could be an issue in the future as the climate changes further, as phenological advances are taking place at different rates (Bartomeus et al., 2011).

1.2 Reversing the loss of flower-rich habitat and flower abundance within agricultural landscapes

It is well accepted that the intensification of agriculture and the loss of suitable and diverse habitat are some of the key contributors to pollinator declines (González-Varo et al., 2013; Goulson et al., 2008; Goulson et al., 2015; Hemberger et al., 2021; Ollerton et al., 2014; Potts et al., 2016). Ollerton et al. (2014) directly link agricultural intensification to pollinator decline. They note that in Britain, a region greatly modified by intensive agricultural practices, extinction rates since the mid-19th century have increased for some pollinator species during periods of major agricultural management and policy changes (Ollerton et al., 2014). In the Midwestern USA, Hemberger et al. (2021) found that a steep decline in *Bombus* species richness coincided with a decrease in the number of different crops grown in the mid-20th century. Additionally, some *Bombus* species (e.g. *B. terricola*) were less likely to occur in a given location as cropped area increased. However, the opposite was true for other species such as *B. impatiens*, which experienced a greater likelihood of occurrence as both the proportion of cropped area and number of different crop types increased (Hemberger et al., 2021). The greater likelihood of occurrence of *B. impatiens* with a greater proportion of cropped land is likely due to its generalist nature, with generalist species likely able to exploit a wider range of crop species and a greater proportion of the flowering plant species following loss of semi-natural habitat (Goulson et al., 2005; Hemberger et al., 2021; Wood et al., 2019).

Other studies strongly indicate that the loss of floral resources, most likely as a result of agricultural intensification, have led to subsequent pollinator declines (Baude et al., 2016; Carvell et al., 2006a; Carvell et al., 2017; Scheper et al., 2014). Intensive agricultural practices can directly reduce the cover of natural or semi-natural habitat (Goulson et al., 2015), but they can also lead to a reduction in available nesting and foraging resources through habitat degradation, for example through agrochemical drift (Potts et al., 2016). Baude et al. (2016) for example, found a significant decrease between 1978 and 2007 in nectar-rich plant species diversity (using a Shannon index of diversity) in British improved grassland and arable land, while Robinson and Sutherland (2002) noted a decline in the seed bank density (seeds/m^2 in top 1cm of soil) of British arable land across the 20th century.

1.2.1 The effect of greater floral resources at the crop-level upon pollinator/pollination metrics

The important role that pollinators play in enhancing yield in many crop species (Klein et al., 2007) demonstrates the enormous value of reversing the impacts of agricultural intensification and, increasing pollinator floral resources in the farmed landscape. Studies have been set up to explore the effect of increasing floral resources upon pollination metrics in nearby pollinator-dependent crops. A meta-analysis by Zamorano et al. (2020), found that the presence of floral resources in margins adjacent to crops led to higher pollinator richness and abundance (effect size estimated using Hedges' *d* index) at the edge of crops, when compared to controls with no floral resources in margins adjacent to crops. However, no significant effect was found when looking at pollinator abundance/richness inside the crop, between crops adjacent to floral resources and those that were not (Zamorano et al., 2020). This could potentially be a result of including studies looking at many different crop types within the meta-analysis. Some crops may be very attractive to pollinators (e.g. blueberry), whereas the floral resources may be more attractive than the crop in other instances (e.g. in the case of cereal crops), leading to an opposite direction of effects (Zamorano et al., 2020). Individual crops have been shown to benefit from the presence of nearby floral resources, as shown by Feltham et al. (2015), one of the individual studies within the meta-analysis. Pollinator abundance (per 100m transect) was found to be greater in polytunnel-grown strawberry crops with wildflower strips established in close proximity, compared to control crops without wildflower strips nearby (Feltham et al., 2015).

The presence of floral resources adjacent to crops was not found to have a significant effect upon crop yield (Zamorano et al., 2020) However, the sample size for studies focusing upon yield (n=8) was small and the effect size was almost significant (P=0.08) (Zamorano et al., 2020), indicating perhaps that a greater sample size and range of crops would have led to a significant effect size. As demonstrated by the small sample size, the authors note the relatively few studies investigating the effect of increasing adjacent floral resources directly upon crop yield, as opposed to proxies such as pollinator abundance in crops (Zamorano et al., 2020). This research gap has also been highlighted by Holland et al. (2017) in the context of landscape complexity, i.e. very few studies focus upon the relationship between landscape complexity / the quantity and quality of semi-natural habitat and, crop yield as a direct measure of the pollination service provided.

Of those studies that do focus upon yield, a meta-analysis by Albrecht et al. (2020) found no significant relationship between crop yield (measured as either fruits/unit area or mass) and the presence/absence of wildflower strips adjacent to crops. As suggested by the authors, this could be due to the complexity of variables contributing to crop yield and which were not accounted for, such as the level of agrochemical application (Albrecht et al., 2020). No distinction was made as to the individual effects of pest control or pollination services upon yield (Albrecht et al., 2020). One way to do this would be to carry out pollinator exclusion experiments implemented in the presence/absence of adjacent wildflower strips as do Blaauw and Isaacs (2014). Blaauw and Isaacs (2014) is one of the individual studies included within the meta-analysis that did demonstrate an effect of wildflower strips upon yield in addition to pollinator abundance. Wild bee and hoverfly abundance (abundance/minute) in the 3rd and 4th years of their study, but not honeybee abundance, was greater in *Vaccinium corymbosum* L. fields adjacent to sown wildflower strips when compared to control fields adjacent to grass strips (Blaauw and Isaacs, 2014). This also translated down to yield (kg/ha), which in the 3rd and 4th years of the study was higher in the fields adjacent to sown wildflower strips when compared to the control fields (Blaauw and Isaacs, 2014).

Albrecht et al. (2020) found no significant difference in the provision of pollination services (measured via metrics such as fruit/seed set and standardised across studies using a z-score) between fields with additional floral resources (both wildflower strips and hedgerow) and those without (Albrecht et al., 2020). Similarly to Zamorano et al. (2020), this outcome may be a result of including different crop types within the analysis, with opposite effects that therefore counteract each other. For example, floral resources may be more attractive than some crops, therefore drawing pollinators away from the crop and decreasing the crop pollination service provision relative to having no adjacent floral resources. In other instances, spill-over of pollinators from floral resources into attractive crops could lead to an increased pollination service provision. In crops adjacent to floral resources, pollination service metrics (fruit/seed set, etc.) were found to decrease as distance to floral resources increased, an effect that was not found within crops with no adjacent floral resources (Albrecht et al., 2020). This suggests that pollinators do potentially spill-over in to crops from adjacent floral resources but that, if only a small proportion of a field experiences increased pollination services, this effect is not visible at the field level.

Despite their important role as crop pollinators, Kleijn et al. (2015) warn against using the contribution of pollinators towards increasing crop production as an argument for their conservation. This is because, when focusing upon bee taxa, crop pollination services globally tend to be driven by a limited suite of already common and abundant species (approximately 2% of bee species in each region) (Kleijn et al., 2015). Results from a study by Nicholson et al. (2020) support this suggestion. Flower mixes sown adjacent to four different crops significantly increased bee species richness (chao1 estimator), diversity (effective number of species) and abundance at the field edge relative to control edges without sown flower mixes. However, bee species richness, diversity and abundance in the crops themselves was not significantly different between fields adjacent to flower mixes, when compared to controls without flower mixes (Nicholson et al., 2020). These outcomes suggest that establishing floral resources in various cropping systems holds potential from a pollinator conservation perspective, but less so from a pollination services perspective, as the effects of floral resources do not spill over into the crops themselves (Nicholson et al., 2020). However, one potential limitation of the study is that the sown flower mixes had been designed to flower following crop bloom. Had the mixes been designed to flower prior to crop bloom (therefore still avoiding competition with the crop), pollinators may have followed the flowering resources into the crop.

Regardless of the extent to which pollination services are enhanced, increasing floral cover, floral diversity and the availability of flower-rich habitat in agricultural landscapes is important for wild pollinator conservation (Goulson et al., 2015; Lowe et al., 2021; Scheper et al., 2015; Vickruck et al., 2021). A meta-analysis by Lowe et al. (2021) found that planted flower-rich interventions (e.g. including hedgerows and wildflower strips) at field boundaries increased both pollinator richness and abundance in field boundaries when compared to controls. These trends hold true even for rare species, with Scheper et al. (2015) demonstrating a greater abundance of Red-List species (in $150m^2$ transects) in sown wildflower strips compared to controls in three out of four European countries and, a greater species richness (in $150m^2$ transects) of Red-list bees in wildflower strips in the UK (Scheper et al., 2015). These studies corroborate an earlier meta-analysis by Scheper et al. (2013), which also found that agri-environmental interventions, including sown wildflower mixes, increased pollinator richness and abundance (estimated using Hedges' *d* index) for a range of pollinator taxa.

1.2.2 Resource provision at the landscape level

Rather than focusing on the field-level floral resource availability, other studies have focused upon landscape complexity and/or semi-natural habitat in the agricultural landscape as a whole and, the relationship with pollinator and pollination metrics (Holland et al., 2017). Using a systematic mapping process focusing exclusively on European studies, Holland et al. (2017) found that the majority of pollinator studies (79%) looking at the effect of semi-natural habitat interventions (e.g. hedgerows) upon pollination/pollinator metrics, demonstrated that the interventions positively affected pollination/pollinator metrics such as abundance. Semi-natural habitat types can also vary according to the effects they have upon pollinator communities. Neumüller et al. (2020) for example, demonstrated that sown flower mixes had a lower wild bee species richness than remnant patches of potentially suitable habitat (for example field margins) or 'near-natural' grasslands.

When assessing the extent to which agricultural landscapes can support different pollinator communities, spatial scale is important. This is shown by Steffan-Dewenter et al. (2002), who demonstrate that bee diversity and abundance are influenced by the proportion of semi-natural habitat at different spatial scales. An increasing proportion of semi-natural habitat was found to be positively linked to solitary bee abundance and diversity at smaller spatial scales and honeybees at larger spatial scales (Steffan-Dewenter et al., 2002). Kohler et al. (2008) studied the effect of distance from nature reserves upon bee and hoverfly abundance in agricultural landscapes (0-300m distance). As the distance to nature reserves increased, bee and hoverfly abundance both decreased. These relationships were driven by significant decreases in hoverfly abundance up to 125m from the nature reserves and decreases in bee abundance between 0 and 100m from the nature reserves (Kohler et al., 2008).

1.2.3 Landscape context moderates the effect of flower-rich interventions

As noted by Lowe et al. (2021), the impact of planted flower-rich interventions upon pollinator metrics has been shown to be moderated by the wider landscape, for example according to the quantity or spatial configuration of natural or semi-natural habitat. Lowe et al. (2021) suggest that the greatest effect size of flower-rich interventions upon pollinator metrics is achieved in landscapes with 10-50% habitat. This suggestion is similar to the findings of Scheper et al. (2013) whereby, simple landscapes with 1-20% habitat benefited the most from agri-environment interventions in terms of higher pollinator abundance and richness (effect size measured using Hedges' *d*), when compared to landscapes completely devoid of semi-natural habitat (<1%) or with large proportions of semi-natural habitat (>20%). One suggested explanation for this outcome is that landscapes completely devoid of semi-natural habitat have few pollinators in the first place to attract to florally-rich interventions. On the other hand, in landscapes with very large proportions of semi-natural habitat, pollinators may be drawn out of floral interventions into the semi-natural habitat. Landscapes with intermediate proportions of semi-natural habitat do have a reservoir of pollinators in the first place, and these benefit from the enhanced resources provided through florally-rich interventions.

Neumüller et al., (2020) found that wild bee richness in three different habitat types (near-natural grasslands, remnant habitat patches and sown flower mixes) was also moderated by the surrounding landscape composition. For example, a significant positive relationship was found between wild bee richness and extensive grassland cover early in the study sampling season (with season spanning April-September) and in the middle of the season. The effect sizes were different in each habitat type, with extensive grassland cover in the early season for example, only significantly affecting bee species richness in remnant habitats and sown flower mixes, but not near-natural grasslands. This outcomes supports the authors' theory that sown flower margins would be more influenced by characteristics of the wider landscape, as they are artificial habitats whose floral resources potentially only meet the foraging requirements of particular groups of bees (Neumüller et al., 2020). As remnant habitats included features such as paths and field margins, it is likely that they were more disturbed habitats than patches of near-natural grassland, which may also have made them unsuitable for certain subsets of the bee community. This perhaps explains why the landscape composition (extensive grassland cover) had a strong effect in this habitat type as well. At the local level, significant positive relationships were found between both floral species richness / floral cover and bee species richness, in addition to a significant positive relationship between floral cover and bee abundance (Neumüller et al., 2020). This study demonstrates the importance of considering the response of pollinators to floral resources at multiple levels, from the local to the landscape.

In terms of increasing the pollination services to flowering crops, the interactions between semi-natural habitat cover and agri-environment interventions also need to be understood. Krimmer et al. (2019) for example, found that in *Brassica napus* L. crops adjacent to small fields (<1.5ha) sown with flower mixes, a greater semi-natural habitat cover (% in 1km radius) led to a larger number of pollinator visits (number of times a pollinator came into contact with a flower stigma in 5 minute observations of $4m^2$ plots) to oilseed rape flowers. This relationship was not found with larger fields (>1.5ha) sown with flower mixes, indicating that the proportion of semi-natural habitat has less of an effect on pollinator flower-visits if alternative resources are available (Krimmer et al., 2019).

From the literature reviewed here in Section 1.2, it is evident that considerations of both floral resource availability at the local scale (Lowe et al., 2021; Neumüller et al., 2020; Scheper et al., 2015) and semi-natural habitat availability at the landscape scale (Holland et al., 2017; Neumüller et al., 2020; Steffan-Dewenter et al., 2002), as well as interactions between the two (Krimmer et al., 2019; Lowe et al., 2021; Scheper et al., 2013), are important to consider when deciding upon the best management interventions for wild pollinator conservation in agricultural landscapes. Vickruck et al. (2021) propose such an approach, i.e. encouraging land managers to employ multi-level management by retaining and maintaining existing areas of habitat, restoring areas of degraded habitat and, enhancing cultivated areas, for example through the inclusion of flower-rich margins.

1.3 Floral resource quality

In Section 1.2, I outlined literature demonstrating increases in the abundance and richness of pollinator species as a result of increasing flower cover/abundance or semi-natural habitat, particularly in resource-poor agricultural landscapes (e.g. Baude et al., 2016; Lowe et al., 2021; Scheper et al., 2013; Scheper et al., 2015). However, Timberlake et al. (2021) warn against the assumption that a greater proportion of flower-rich habitat or a greater floral abundance equates to a greater availability of within-habitat foraging resources such as nectar and pollen. In their study for example, no relationship was found between the farm-level nectar sugar supply (g/km^2/day) and proportion of semi-natural habitat (% of total area), indicating that the former cannot be estimated from the latter (Timberlake et al., 2021).

At the simplest level, it is the availability of forage resources such as nectar and pollen, as well as their nutritional profiles, that contribute to the health and viability of pollinator communities (e.g. Alaux et al., 2010; Vaudo et al., 2020; Woodard and Jha, 2017). Nectar sugar constitutes the prime energy source available to pollinators, while pollen provides essential macro and micronutrients in the form of lipids, proteins, vitamins and minerals (Kämper et al., 2016; Baude et al., 2016; Vaudo et al., 2016; Woodard and Jha, 2017). A greater pollen protein concentration for example, leads to greater larvae weight (Roulston and Cane, 2002), while pollen species with a poorer nutritional composition (e.g. lower % of proteins and mass of amino acids) can lead to a lower survival rate (%) over time (Di Pasquale et al., 2013). The nutritional composition of foraging resources can also negatively affect long-term pollinator viability. Kämper et al. (2016) found a negative relationship between the concentration of amino acids in pollen (µg/mg dry weight of pollen) stored by *Bombus terrestris* colonies and, growth of those colonies. However, a positive relationship was found between the overall quantity of stored protein and colony growth (Kämper et al., 2016). As noted by the authors, this indicates that larger quantities of a lower quality pollen are preferable for *B. terrestris* colonies, perhaps due to their generalist nature that allows them to exploit multiple species that are flowering in abundance.

There are situations in agricultural landscapes where flower abundance can be very high but floral diversity is low, for example during the mass-flowering of crops such as *Brassica napus* L. (Goulson et al., 2008; Moerman et al., 2017; Vaudo et al., 2015). Goulson et al. (2008) likened the lack of floral diversity available to pollinators in such a situation as being equivalent to humans only eating one food item each month: we would not obtain the full suite of nutrients required to maintain optimal health. Moerman et al. (2017) demonstrate that monofloral pollen diets can be adequate if their nutrient profile is suitable for a particular pollinator species. However, a variety of floral resources can provide the diversity of nutrients required to maintain pollinator health and performance across different species (Alaux et al., 2010; Vaudo et al., 2020; Woodard and Jha, 2017) and, bees have been shown to selectively forage based on the nutritional provision of floral resources (e.g. Cnaani et al., 2006; Ghosh et al., 2020; Vaudo et al., 2016; Vaudo et al., 2020).

Various studies for example, have demonstrated preferential foraging of bees for pollens with high protein contents (e.g. Ghosh et al., 2020; Hanley et al., 2008). Leonhardt and Blüthgen (2012) found that *Bombus* species foraged for pollen containing a significantly greater quantity of protein (µM amino acids / g pollen [dry weight]) than pollen foraged by *Apis mellifera*. Ruedenauer et al. (2020) found a reduced pollen consumption by *Bombus terrestris* as fatty acid concentration in pollen diets increased. Vaudo et al. (2020) demonstrated a preferred pollen protein:lipid ratio of 4:1 for *Bombus impatiens*, while for *Apis mellifera* the preferred ratio ranged from 1:1 to 2:1, indicating that *Apis mellifera* and *Bombus impatiens* would be expected to use a different suite of floral species.

Easily metabolisable sugars are the key nutrients provided to nectar foragers (Willmer, 2011). The potential energy intake by a flower visitor after one nectar foraging visit can be obtained based on the sugar concentration and nectar volume and, as with pollen, bees will selectively forage the most rewarding resource (Cnaani et al., 2006; Willmer, 2011). Cresswell et al. (1999) demonstrated for example that, as the volume of a sugar syrup 'nectar' increased in experimentally manipulated *Brassica napus* flowers, the length of time *Bombus lapidarius* spent foraging at individual flowers also increased. Bailes et al. (2018) found that *Bombus terrestris* preferentially foraged a sugar solution with a 55% sugar concentration as opposed to a 40% concentration. However, when presented with a choice of 55% or 68% sugar concentrations, no preferential foraging was found (Bailes et al., 2018).

While a greater nectar sugar concentration increases the viscosity of the sugar solution, which can slow down nectar ingestion (Harder, 1986). Harder (1986) noted for example, a critical threshold of approximately 41% sucrose concentration above which the rate of ingestion of *Bombus* species decreased. However, net energy intake rate is a function of both the nectar ingestion rate and the nectar energy content (sugar mass), the latter increasing as nectar sugar concentration increases. The nectar sugar concentration that provides the greatest rate of net energy intake therefore ranges from 50-65% concentration (Harder et al., 1986), explaining the preferential foraging of a 55% nectar sugar concentration by Bailes et al. (2018).

Nectar sugar concentrations that optimise the rate of energy intake vary according to nectar foraging technique (Kim et al., 2011; Vaudo et al., 2015). Kim et al. (2011) found a modelled sugar concentration value of 52% to be optimal when 'viscous dipping' is employed, as is the case with *Bombus* for example and similar to Harder et al. (1986). Other studies demonstrated that for 'active suction' foragers, which include many lepidopterans, the optimal sugar concentration ranges between 30% and 40% (Kim et al., 2011).

While less studied, other nutrients such as amino acids are also present in nectar and pollinators may selectively forage for these (Broadhead and Raguso, 2021; Nepi, 2014; Vaudo et al., 2015). Broadhead and Raguso (2021) found that the hawkmoth *Manduca sexta* showed a tendency to innately prefer artificial nectar solutions that contained amino acids, although this preference was not quite statistically significant (p=0.06). On the other hand, following associative learning in which *M. sexta* moths learnt to associate blue and yellow artificial flowers with different nectar treatments, *M. sexta* demonstrated a significant preference (p=0.01) for artificial nectar containing amino acids at a 25% sucrose concentration (Broadhead and Raguso, 2021).

The diversity of floral rewards provided through different flowering plant species and, the selective foraging of pollinators to meet particular nutritional requirements (Vaudo et al., 2015), highlights the need to switch the focus from looking solely at the effect of floral abundance/diversity, to also looking at the effect of floral resource availability on pollinator metrics (Timberlake et al., 2021). Nectar sugar is a good starting point when it comes to studying the effects of resource availability upon pollinators. This is because, as mentioned previously, it is the primary source of carbohydrate in the pollinator diet and is needed to fuel their remaining activities including foraging flight (Baude et al., 2016; Willmer, 2011). Baude et al. (2016) follow this reasoning. They also employ the quantity of nectar sugar produced per flower (µg/flower/day) as a function of nectar volume and concentration as, it provides a unit that can be compared between species and therefore determine those that are most rewarding to pollinators (Baude et al., 2016). Furthermore, although many authors have started assessing the provision of various pollen macro and micronutrients by different flowering plant species (e.g. Weiner et al., 2010), there are large gaps in this knowledge. Pollen databases do exist for the UK (Timberlake et al., 2021), but these are not publically available. For the UK however, Baude et al. (2016) provide a database of nectar sugar supply rates (µg/flower/day) for 270 species. This includes 220 or 48% of species that contributed 99% of the British plant cover according to the 2007 Countryside Survey (Carey et al., 2008), in addition to a further 50 locally relevant species (Baude et al., 2016). The remaining 52% species are unlikely to contribute any pollinator forage rewards, as they include for example, gymnosperms, bryophytes, etc. (Baude et al., 2016). This database is also complemented by data from additional studies (e.g. Hicks et al. 2016; Timberlake et al., 2019). These resources combined are therefore likely to cover the majority of flowering plant species that we would encounter in an arable landscape within Great Britain (Baude et al., 2016). For these reasons I choose to focus on the nectar sugar availability within UK agricultural landscapes in this PhD project. I address the key aims of this project in the following sections.

1.4 Methods for estimating the nectar sugar resource available to pollinators at the habitat and landscape and within-habitat scale

Studies have started to estimate the nectar sugar supply available to pollinators at the national (Baude et al., 2016), landscape (Jachuła et al., 2021; Langlois et al., 2020; Timberlake et al., 2021) and individual habitat level (Hicks et al., 2016; Holl et al., 1995). For example, Baude et al. (2016) calculated changes in the nectar sugar supply at a national level for the whole of Great Britain between the 1970s and 2000s. The nectar sucrose (µg/flower/24hrs) was collected from flowers following 24 hrs of excluding access to flower-visiting insects. The density of open flowers was calculated using 0.25m^2 quadrats placed over populations of each flowering species, or within 0.13m^3 cubes (0.5x0.5x0.5) for tree species, and a triangular function was used to account for floral density variation across the season. These data were then scaled up to the annual quantity of nectar sugar produced per unit area, or modelled where field-data were missing. The nectar sugar supply was then scaled-up to the individual habitat (11 habitats including arable land, calcareous grassland, etc. in addition to linear features) and national level, using Countryside Survey data (Baude et al., 2016). The Countryside Survey involved the random sampling of $1km^2$ sites across Great Britain. Within these sites, vegetation surveys for linear features (e.g. hedgerows) and habitats were carried out to estimate the plant species composition and extent of cover in each habitat type (Carey et al., 2008).

A decline in nectar sugar productivity (kg/ha/year) was observed for arable landscapes between 1978 and 1990 (Baude et al., 2016), potentially coinciding with shifts in agricultural policy in the 1970s that led to a greater intensification of agricultural practices (Baude et al., 2016; Robinson and Sutherland, 2002). Productivity then remained stable until 1998, before increasing again between 1998 and 2007 (Baude et al., 2016). This was again a potential result of changing agricultural policy; this time the introduction of UK agri-environment schemes such as the 'Countryside Stewardship Scheme' that was introduced to England in 1991 with aims, among others, of improving existing habitat and creating new (Ovenden et al., 1998). The publication from 1995 onwards of British Biodiversity Action Plans for at-risk species also included specific agri-environment action points such as maintaining species-rich hedgerow (Ovenden et al., 1998).

The diversity of nectar sources in arable landscapes on the other hand, continued to decline between 1978 and 2007 (Baude et al., 2016). Over time therefore, the ability for many pollinators in arable landscapes to selectively forage for their preferred nectar compositions and obtain a balanced diet may have reduced (Bailes et al., 2018; Kim et al., 2011; Vaudo et al., 2015). For example, 30% of the total British nectar supply is produced by *Trifolium repens* (Baude et al., 2016) in the Fabaceae family. The deep nectar tubes of *T. repens* likely preclude the use of this species by pollinators with short mouthparts (Baude et al., 2016; Klumpers et al., 2019).

A number of other studies have used the nectar sugar data for flowering plant species acquired by Baude et al. (2016), while supplementing data for species missing from the database using the same methods (Langlois et al., 2020; Tew et al., 2021; Timberlake et al., 2021). Despite many studies relying on this resource, a number of limitations do need to be recognised. Nectar sugar data values for each plant species were gathered from 1-2 sites and on different dates if possible (Baude et al., 2016). Given the variability in nectar sugar production even within the same species (e.g. Bailes et al., 2018), it is unlikely that the nectar sugar production values remain constant across Great Britain (or Europe in the case of Langlois et al., 2020), or that their variability is captured by this small sample. The floral density per unit of vegetative cover estimates for each plant species were also collected across a median of 10 quadrats, which is again not a large dataset for the entirety of Great Britain. Nectar sugar and floral density surveys across additional regions of Great Britain and beyond, should therefore be an urgent research priority. In the meantime however, the database provided by Baude et al. (2016) is the most comprehensive nectar sugar database available for Great Britain, with Timberlake et al. (2019) and Hicks et al. (2016) providing additional data for a few missing species. These are the datasets that I use throughout this PhD.

Tew et al. (2021) compared the nectar sugar production (μg/m^2/day) of three key landscape categories (farmland, nature reserves and urban). Transects were used to sample floral abundance in each habitat type within 12 sites respectively for each landscape category. At each site, 100 quadrats were sampled, allocated to each habitat based on their proportional abundance. Nectar sugar production was then scaled up to the landscape level by multiplying nectar sugar production data (either from literature or collected through this study, empirically or modelled) by the floral abundance data. No significant difference was found between each landscape type in terms of the nectar sugar quantity produced (μg/m^2/day) (Tew et al., 2021).

In a Belgian study, Langlois et al. (2020) calculated the nectar sugar production values within 1km radius landscapes of two different types (intensively-farmed and extensively farmed). Nectar sugar production values per flower were again obtained from the literature (Baude et al., 2016; Hicks et al., 2016). Within 1km radius landscapes, the landscape-level flower abundance for a particular flowering plant species was estimated by multiplying the surface area of each habitat type by the average floral density of the flowering plant species within the same habitat type and summing the values for each habitat. Flower abundance for each flowering plant species was then multiplied by the nectar sugar production values and summed to find the total nectar-sugar production values for each landscape. A significant difference in the nectar sugar production (g/ha) was found between habitat types, between months and in the month x habitat type interaction, demonstrating that the relative nectar resources in each habitat type vary according to the time of year (Langlois et al., 2020). This is potentially why no difference in nectar sugar production (g/ha) or pollinator abundance was found between landscape types ('extensive' which consisted of >10% organic crops or extensive grasslands and 'intensive' which consisted of <10% organic crops or extensive grassland). The combined nectar resources at different times of year provided by all the different habitats present in each landscape type in varying proportions may have been counterbalancing one another. For example, intensively-managed crops had a higher nectar sugar production value in May (138g/ha) than organic crops (6g/ha), whereas the reverse was true in June (27g/ha and 2052g/ha for intensively-managed and organic crops respectively) (Langlois et al., 2020).

Timberlake et al. (2021) surveyed floral resources at four time-points between July 2017 and May 2018 in 1km radius sites at each of 12 farms. The mean floral unit abundance (units/m^2) in each habitat type present at an individual farm was estimated through quadrat surveys carried out along six transects within each habitat type present at an individual farm. Floral unit abundance of each species in each habitat was then multiplied by nectar sugar production values from the literature (Baude et al., 2016; Timberlake et al., 2019) and summed to obtain a total nectar sugar quantity for each habitat which was then scaled up to the farm-level, based on the area of each habitat in the 1km radius. A significant effect of nectar sugar production (g/km^2/day) in September upon *Bombus terrestris* colony density (colonies/km^2) the following summer was observed (Timberlake et al., 2021), likely because queens are building up supplies for hibernation at this time of year.

Jachuła et al. (2021) measured nectar sugar availability according to different habitat types in the Lublin Upland region of Poland. Fallow land contributed the greatest quantity of nectar sugar per m^2. Data were also scaled up to estimate nectar sugar provision at the landscape level and compared to the nectar sugar demand of bumblebees and honeybees as estimated from the literature (Jachuła et al., 2021).

While each of these studies do estimate the habitat-level nectar sugar supply, they do not focus on the fine-scale variability of nectar sugar within the same habitat type. For example, even wildflower mixes of the exact same composition but sown in different locations, can result in different proportions of floral units of individual species, and consequently different nectar sugar supplies, simply due to environmental variation (Hicks et al., 2016). Hicks et al. (2016) do focus on within-habitat variability by comparing the nectar sugar and pollen production across and within annual and perennial commercially-available mixes (designed to provide an abundant supply of nectar and pollen-rich floral resources) and controls, the latter consisting of amenity grassland. Both perennial and annual mixes produced a significantly greater quantity of nectar sugar and pollen when compared to controls (Hicks et al., 2016). Annual mixes produced less nectar sugar and pollen than perennial mixes (Hicks et al., 2016).

Hicks et al. (2016) do not relate their nectar sugar data to any pollinator metrics. They also focus on wildflower mixes sown within an urban environment. The within-habitat nectar sugar variability of habitats commonly found within agricultural landscapes is therefore a research gap that I propose to start addressing through this PhD project. The first aim of my PhD thesis is to determine whether the nectar sugar supply (mg/m^2/day) across arable field margins is correlated with bee abundance (see Section 1.9 thesis aims for more detail).

1.5 Spatial and temporal variation of floral resources within landscapes

The availability of pollen and nectar is not static within a landscape over time and therefore does not necessarily match the phenological patterns of pollinators inhabiting the same landscape (e.g. Jachuła et al., 2021; Timberlake et al., 2019). Timberlake et al. (2021) for example, found that across 12 mixed farm systems, the species providing 75% or more of the nectar supply varied with time of year. Species such as *Bellis perennis* and *Lamium purpureum* constituted important nectar resources in early spring and *Cirsium arvense*, *Rubus fruticosus* and *Trifolium repens* were the highest nectar producers in the summer (Timberlake et al., 2021). In a Mediterranean context, Flo et al. (2018) found that nectar sugar production in a Natural Park in Spain varied significantly according to both year and month. Baude et al. (2016) found that the greatest proportion of the British annual nectar supply was produced in July/August. This is similar to Hicks et al. (2016), who found nectar production to be highest in early August, in Edinburgh-based urban meadows sown with a perennial mix. On the other hand, those authors found a lack of floral resources at their study sites between March and May (Hicks et al., 2016).

To enable a wide diversity of pollinators to meet their nutritional requirements, discussed above in Section 1.3, adequate supplies of nectar and pollen must be available throughout the year, in a temporal pattern that matches the phenological pattern of pollinator demand (Balfour et al., 2018; Jachuła et al., 2021; Timberlake et al., 2019). This does not always happen, as demonstrated by Timberlake et al. (2019) who found that nectar sugar supply (g/bee/km^2/day) across three farms in the south-west UK and, the nectar sugar demand (g/bee/km^2/day) of three *Bombus* species commonly found in UK agricultural landscapes, did not match at certain times of year such as in March. The nectar sugar demand of *Bombus* colonies was calculated based on data from the literature available for *B. terrestris* (Heinrich, 1979; Rotheray et al., 2017), which was assumed to be similar for the remaining two species, *B. lapidarius* and *B. pascuorum* (Timberlake et al., 2019). Colony density estimates for each of the three species were also identified from the literature (Dicks et al., 2015). Jachuła et al. (2021) also demonstrated a discrepancy between bumblebee and honeybee nectar sugar demand and landscape supply at certain times of year, with the nectar sugar production in March and June being lower than required.

The spatial distribution of floral resources is also an important consideration. Nectar-rich flowering plant species need to be well-distributed across a landscape to lie within the diverse foraging ranges of different pollinator species (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007; Zurbuchen et al., 2010). Larger bees such as *Bombus* species and *Apis mellifera* can travel large distances when foraging, up to several kilometres (e.g. Beekman and Ratnieks, 2000; Couvillon et al., 2015; Greenleaf et al., 2007). Many solitary species travel shorter distances of only several hundred metres when foraging, although foraging ranges vary according to the size of individuals and can still be greater than a kilometre (Greenleaf et al., 2007; Zurbuchen et al., 2010).

A baseline assessment of the floral resources available to pollinators throughout the year and their distribution within a landscape, would allow any resource gaps to be addressed. In an agricultural context for example, suitable agri-environment interventions could be selected or, existing agri-environment interventions could be managed to increase the supply of floral resources at particular times of year. Dicks et al. (2015) note for example that, sown interventions available as options in UK-based agri-environment schemes such as Countryside Stewardship rarely provide floral resources in the early spring (March/April). For reference, Countryside Stewardship is a financial incentive scheme that rewards farmers for implementing various measures that protect and conserve wildlife and the wider environment (UK Government, 2021c).

Countryside Stewardship options such as the 'AB1 – Nectar flower mix' option (UK Government, 2021b) allow some flexibility when it comes to choosing which species to include in a wildflower mix. Species that flower earlier in the year could subsequently be selected, e.g. *Taraxacum officinale*, *Primula vulgaris* or *Silene dioica* (Dicks et al., 2015; Nowakowski and Pywell, 2016). Hedgerows are also an important source of spring-flowering floral resources (Baude et al., 2016; Dicks et al., 2015) and these could be managed to increase the floral abundance of nectar-rich flowering plant species, such as *Crataegus monogyna* or *Prunus spinosa* (Baude et al., 2016). This could be done for example through changing the hedgerow cutting regime, with Staley et al. (2012) demonstrating that when *Crataegus monogyna* hedgerow is cut every 3 years, floral abundance is 2.1 times greater than when it is cut every year.

The traditional way to estimate the abundance of floral resources is through quadrat surveys. These have certain limitations (Willcox et al., 2018). Quadrat surveys can be time-consuming and they can be hard to carry out in certain habitat types or potentially impossible to carry out in remote or inaccessible locations (Barnas et al., 2019). Furthermore, a sub-set of an area is surveyed through the random positioning of quadrats and data are then amalgamated to obtain a mean unit value (e.g. floral units / m^2 or proportion of floral cover / m^2) across the whole area (e.g. see Hicks et al., 2016). In other words, the true distribution of the unit being surveyed is only estimated from a sample. An alternative to carrying out quadrat surveys would be to use remote sensing techniques that allow a map of the distribution of floral resources to be estimated. The second key aim of my PhD thesis is therefore to determine whether nectar-rich flowering plant species can be mapped using high-resolution (3cm and 7cm spatial resolution) remotely-sensed multispectral imagery. I describe this further in the following section.

1.6 Remote sensing as an alternative to on-the-ground surveys for measuring floral resources

In Section 1.5 above, I considered the value of having a baseline assessment of the spatial and temporal distribution of floral resources so that gaps in pollinator foraging resource availability can be addressed (e.g. Balfour et al., 2018; Jachuła et al., 2021; Timberlake et al., 2019) or, to feed into spatially-explicit models (e.g. Gardner et al., 2020; Häussler et al., 2017; Lonsdorf et al., 2009). A potential alternative to carrying out ground-truth surveys is the use of remotely-sensed data, such as multispectral imagery acquired via UAV, satellite or manned aircraft platforms, for classifying habitats, flowering plant species or other features of importance to pollinators (Willcox et al. 2018). Remotely sensed data has been applied in a number of ways to address ecological questions and inform conservation-related decisions (Pettorelli et al., 2018a). Applications include, among many others, monitoring invasive plant species (e.g. Dash et al., 2019; Matongera et al., 2017; Michez et al., 2016; Müllerová et al., 2017), assessing the extent of deforestation or other land-use/land-cover change (e.g. Potapov et al., 2012) and, estimating species distributions (e.g. Fretwell and Trathan, 2021; Luoto et al., 2002).

Remote-sensing surveys can address some of the aforementioned issues with traditional quadrat surveys, such as the time and labour-consuming nature of the fieldwork involved, as well as difficulties involved with surveying inaccessible locations (Barnas et al., 2019; Willcox et al., 2018). Such surveys can be carried out in areas not accessible by foot, data can be acquired relatively quickly if not much time is available for fieldwork, acquisition can occur across large geographical areas and, they can be more representative of the actual spatial distribution of the features being measured (Barnas et al., 2019; Henrys and Jarvis, 2019).

1.7 Basic principles of remote sensing

A range of platform types are available for acquiring remotely-sensed data including satellites, manned aircraft and unmanned aerial vehicles (e.g. see Bradter et al., 2020; Feilhauer et al., 2013; Sankey et al., 2018; Schmidt et al., 2018). Data are subsequently acquired via one of these platforms using a variety of sensors which fall into two key categories (Lillesand et al., 2015; Melin et al., 2017). 'Active' sensors include LiDAR (light detection and ranging), whereby a laser pulse is emitted and the time taken for the pulse to be reflected and return to the sensor is used to construct a three-dimensional representation of the survey area (Lefsky et al., 2002; Melin et al., 2017). Active sensors were not used for this research and will not be considered further. 'Passive' sensors on the other hand record the electromagnetic (EM) radiation originating from the sun that is reflected towards the sensor from features upon the Earth's surface (Lillesand et al., 2015). The reflected radiation is recorded in different ranges of the EM spectrum, known as wavelength bands (Lillesand et al., 2015). Multispectral data consist of a few wide bands of data, for example red, green and blue bands in the visible EM spectrum range, as well as infrared bands (Lillesand et al., 2015). Hyperspectral data comprise hundreds of bands, with each constituting a small range of wavelengths from across the EM spectrum (Kattenborn et al., 2019). Data for each wavelength band is collated in a grid of pixels representing the surveyed area and can be stacked into a digital image (Lillesand et al., 2015).

The spatial resolution of pixels in remotely-sensed imagery varies considerably. The European Space Agency's Sentinel-2 satellite platform acquires data with spatial resolutions ranging between 10m and 60m (ESA, 2021) for example, while the PLANET satellites can acquire data with a 0.5m spatial resolution (Planet Labs, 2021). Very-high spatial resolution data with pixel sizes of only a few cm^2 can be acquired using airborne sensors (e.g. Sankey et al., 2018; Xavier et al., 2018). The raw data or radiance recorded by multispectral/hyperspectral sensors consist of the EM radiation reflected by the feature of interest combined with atmospheric interference. The radiance recorded at the sensor in each wavelength band is stored for each pixel as a digital number (DN), with the range of DNs available depending on the 'depth' of information that can be stored in each pixel by the sensor, also known as the radiometric resolution (Lillesand et al., 2015). 8-bit data for example, allows DN values to range from 0-255 while 16-bit data means that DN values can range between 0-65535 (Lillesand et al., 2015). Many studies carry out an atmospheric correction (e.g. see Berk et al., 1998; Smith and Milton, 1999) which removes the atmospheric effects and gives a true reflectance value (as a percentage) for each wavelength band in each pixel.

Remotely sensed image data can be classified using a range of algorithms to produce an output that maps the location of different categories of interest, for example different land use / land cover categories (Lillesand et al., 2015). Later in this project, I employ multispectral imagery acquired via passive sensors with differing spatial resolutions, which I classify using supervised classification approaches (see Section 1.9 below and Chapters 3 and 4). In a supervised classification, pixels known to represent different classification categories on the ground, for example soil, water or vegetation, are used to train a classification algorithm so that it learns the spectral characteristics of each respective classification category (Lillesand et al., 2015). The classification algorithm is then applied to the whole image and, based on the spectral information provided, it allocates each pixel to a classification category. Traditional parametric supervised classifiers such as minimum distance or maximum likelihood take into account the distribution of spectral values of pixels in a training set (Lillesand et al., 2015). Maximum likelihood for example, assumes a normal distribution of spectral values for each classification category in each wavelength band and based on this distribution allocates each pixel in the image to the classification category that it is statistically most likely to belong to (Lillesand et al., 2015). However, it is now also common to use non-parametric classifiers, such as random forest (Breiman, 2001), which do not make any prior assumptions as to data distributions (Belgiu and Drăguţ, 2016; Laryet al., 2016; Lu and Weng, 2007). In this PhD project I use both maximum likelihood and non-parametric classifiers, which I subsequently discuss further in Chapters 3 and 4.

Once a classification output has been produced, its accuracy is assessed. Constructing error matrices is a widely employed method for assessing the classification accuracy of traditional hard classifiers such as maximum likelihood whereby; overall accuracy, user's accuracy and producer's accuracy metrics are calculated (e.g. Lillesand et al., 2015; Olofsson et al., 2013; Sankey et al., 2017, Schmidt et al., 2018). In a pixel-based error matrix, the overall accuracy (%) informs you as to the proportion of a set of verification pixels that have been correctly classified. The user's and producer's accuracies provide a better idea of how well an individual species is being classified. For *n* number of pixels classified as a particular category *X*, user's accuracy (%) tells you the proportion of those classified pixels that have been correctly allocated to category *X*. In other words 100% - user's accuracy = commission error (%) (Olofsson et al., 2013). Producer's accuracy (%) tells you for *n* number of pixels within a remotely-sensed image that are known to belong to a category *X* on the ground, the proportion of those pixels that have correctly been classified as *X*. In other words, 100% -producer's accuracy = the omission error (%) (Olofsson et al., 2013). We can also obtain the area and proportion of a classification map belonging to each classification category. An area-based error matrix allows this area estimate to be adjusted. It takes into account commission and omission error and the relative proportions of a map belonging to different classification categories, to then give a more refined estimate for the area belonging to a category *X* on the ground (Olofsson et al., 2013).

1.8 The potential of remote sensing for mapping pollinator resources

Many studies have benefitted from the numerous satellite platforms providing freely available imagery to gain information about vegetation or different land cover categories (e.g. see Raab et al., 2020; Schmidt et al., 2018). Schmidt et al. (2018) for example, used a combination of European Space Agency Sentinel-1 Synthetic Aperture Radar and Sentinel-2 multispectral imagery to map heathland habitats in Germany. Luoto et al. (2002) used multispectral Landsat satellite imagery classified into different land cover types to assess whether habitat composition and structure, combined with semi-natural grassland connectivity and topographical data, could be used to predict the distribution of a butterfly species (*Parnassius mnemosyne* L.). A logistic regression model was subsequently used to predict the presence of *P. mnemosyne* with accuracies ranging between 92-98%, depending on geographical location (Luoto et al., 2002).

Feilhauer et al. (2013) demonstrated the potential of multispectral satellite data for classifying within-habitat plant compositions. Spectrometer data was simulated to represent multispectral satellite imagery of various spectral and radiometric resolutions (e.g. simulated data with four visible and 1 near-infrared band and an 11-bit radiometric resolution like IKONOS satellite imagery). An Isometric Feature Mapping ordination approach was used to describe the gradual changes in species composition along a gradient in three habitat types (floodplain meadow, nutrient-poor grassland and wet heath), for example, the gradual shift from *Holcus mollis*/*Agrostis capillaris* dominated patches to *Calamagrostis epigejos* dominated patches in nutrient-poor grassland. The floristic composition gradient for each habitat type, as described through the ordination output was modelled against the simulated sensor spectra and the R^2 values of model fit demonstrated how well each sensor could detect the shift in vegetation composition along each gradient. Each simulated multispectral sensor was able to explain species composition adequately for both floodplain meadow and nutrient-poor grassland habitats (R^2 model fits ranging between ~0.55 and 0.75). Only sensors that also acquired information in the short-wave infrared region as well as near-infrared region were able to adequately explain species composition in the wet heath habitat (R^2 model fits ranging between ~0.58 and 0.76).

Pollinator/pollination research has also drawn upon satellite imagery or land cover products derived from satellite imagery (Willcox et al., 2018), for example to scale up field measurements of the floral resource abundance to the national level so that the national nectar-sugar supply (kg/ha/year) can be estimated (Baude et al., 2016; reviewed in Section 1.4). Carrié et al. (2018) investigated the relationship between landscape variables (slope and proportion of sparse vegetation as estimated via the proportion of bare ground) and bee abundance/richness in crop fields (Carrié et al., 2018). The proportion of sparse vegetation in grassland was estimated using an unsupervised classification technique (classes are not defined prior to the classification process but during the classification process, based on similar spectral classification patterns) applied to a normalised difference vegetation index (NDVI) layer. The NDVI layer was calculated from the red and near-infrared imagery layers acquired via the Pleiades satellite platform (Carrié et al., 2018). Vegetation indices use the ratio between values in different wavelength bands to enhance spectral features of interest and minimise noise in other areas (Lillesand et al., 2015). NDVI is a vegetation index that facilitates the distinction of green vegetation from others features within the imagery including soil (Fang and Liang,

2008) and, bare ground or areas of sparse vegetation are therefore also visible within NDVI layers thanks to their low NDVI values (Carrié et al., 2018). Slope values were calculated using a digital terrain model acquired using aerial photography (Carrié et al., 2018). Positive significant relationships were found between both bee abundance and mean grassland slope and between species richness and mean grassland slope. No significant relationship was found between the proportion of sparse vegetation and bee abundance or richness although, when bee data were broken down according to traits, oligolectic bee abundance was found to increase as sparse vegetation (%) increased. As noted by the authors, the oligolectic species consisted entirely of Eucera and Andrena genera, both of which have been shown to nest in bare ground (Potts et al., 2005) and, the result was therefore not surprising (Carrié et al., 2018).

In a Californian study, Leong and Roderick (2015) found that as satellite-derived Enhanced Vegetation Index (EVI - a vegetation index that enhances the detection of green vegetation further and is sensitive in areas with a high vegetation biomass; Fang and Liang, 2008) values in natural habitat sites (comprising mostly oak woodland and grassland) increased, bee abundance also increased. This is likely because higher EVI values are linked to green vegetation which in California correlates with an abundance of flowers (Leong and Roderick, 2015). An extensive number of studies have used satellite and other sources of remotely sensed imagery to determine the landscape structure or composition, for example the proportion of different land cover/habitat types, in the region surrounding pollinator survey sites (e.g. Carrié et al., 2018; Krimmer et al., 2019; Neumüller et al., 2020; reviewed by Willcox et al., 2018). This allows, for example, the moderating effect of the wider landscape on pollinator abundance to be determined as reviewed in Section 1.2.3 (Krimmer et al., 2019; Neumüller et al., 2020).

Despite the wide applicability of satellite remotely sensed data, a key limitation is spatial resolution. Although some satellite platforms can successfully acquire data with a sub-metre resolution (Planet, 2021), many of the available satellite platforms acquire imagery with pixel sizes starting in the several square metres range and increasing from there (ESA, 2021; NASA, 2021). This makes it difficult to identify individual plants, a breakdown of their features such as flowers or, detailed community compositions (Sankey et al., 2018, Neumann et al., 2020, Galbraith et al., 2015, Bradter et al., 2020). Many studies use airborne imagery, with far higher spatial resolutions, to avoid these limitations. Sankey et al. (2018) demonstrate the applicability of using Unmanned Aerial Vehicle (UAV) hyperspectral imagery with 6cm pixel resolution for classifying individual plant species. They achieve overall classification accuracies of 72% and 76% for their semi-arid grassland and desert shrubland sites respectively (Sankey et al., 2018). Bradter et al. (2020) determined the accuracy with which different vegetation communities could be classified using airborne hyperspectral data with a 1mX1m spatial resolution. Random forest classifications were carried out at different levels of thematic resolution. For example, vegetation communities were grouped into different combinations of British National Vegetation Classification categories and, mean overall classification accuracies for these British National Vegetation categories ranged between 84% and 87% (Bradter et al., 2020). Multispectral data were also simulated from the hyperspectral data to represent bands from the Sentinel-2 (13 bands) and Landsat (8 bands) satellite platforms (Bradter et al., 2020). These achieved lower classification accuracies than hyperspectral data, although only marginally lower for the simulated 13-band data (83-86%). Overall accuracies for the simulated 8-band data ranged between 77-85%.

Studies have also started using very-high resolution remote sensing to focus upon the floral component of individual plant species, particularly for mapping invasive species (e.g. Michez et al., 2016) or crop flowers (e.g. Horton et al., 2017), but also for estimating the floral resource available to pollinators (Carl et al., 2017). Imagery acquired via UAV or manned aircraft has been used to detect peach (Horton et al., 2017), *Robinia pseudoacacia* L. (Carl et al., 2017) and *Acacia longifolia* (de Sá et al., 2018) flower pixels and, patches of *Ridolfia segetum* (Peña-Barragán et al., 2007). Spectroradiometer data have been used to estimate the extent of *Halerpestes tricuspis* flower cover (Chen et al., 2009). Michez et al. (2016) used an object-based image analysis approach to classify *Heracleum mantegazzianum* and patches of flowering *Impatiens glandulifera*. Neumann et al. (2020) demonstrated that different life-cycle phases of heathland species *Calluna vulgaris* can be monitored using UAV imagery with a pixel size of approximately 2 cm.

Despite these various studies, Landmann et al. (2018) noted that remote sensing research aiming to map the floral component of individual flowering plant species remains limited. This is despite the potential value of remote sensing technology for determining the floral resources available to pollinators (Szigeti et al., 2016). Xavier et al. (2018) for example, demonstrated that both floral area as estimated through UAV classifications and, floral unit counts obtained via quadrat surveys, were significantly related to pollinator flower visits. However, they did not focus upon individual flowering plant species (Xavier et al., 2018). Using remote sensing imagery to map the floral component of individual plant species that provide important pollinator foraging resources within agricultural landscapes could help in the identification of spatial and temporal gaps in pollinator foraging resources (see Section 1.5).

Furthermore, classification outputs would be useful inputs for spatially-explicit models that estimate pollinator abundance or pollination services (e.g. Gardner et al., 2020; Lonsdorf et al., 2009). Spatially explicit models have been developed and used to predict pollinator metrics such as abundance, or the provision of pollination services according to landscape structure (Gardner et al., 2020; Häussler et al., 2017; Kennedy et al., 2013; Lonsdorf et al., 2009). The model developed by Lonsdorf et al. (2009) for example, requires land use / land cover maps with estimated foraging and nesting resources in each land cover type as inputs, as well as information on the foraging distance of different wild bee species. Foraging and nesting resources within individual cells are subsequently estimated. According to the availability of nesting resources in each cell, and floral resource availability in surrounding cells, the relative abundance of each bee species is estimated for each cell and, a map of the relative bee abundance across a landscape of interest is produced as a model output (Lonsdorf et al., 2009). The floral resources provided by surrounding cells are weighted according to cell distance and the foraging distances of different bee species. A pollination services map is produced as a second model output. This is produced using the first model output and the foraging distances of different bee species, to estimate the relative abundance of each bee species or functional group in individual map units across each farm within a landscape (Lonsdorf et al., 2009). If information is available as to the crop species present in an individual cell and its pollinators, any species that are not known to be pollinators of the crop will be excluded from the pollination services map (Lonsdorf et al., 2009).

One limitation of the Lonsdorf et al. (2009) model is that the assumption is made that bee species forage equally in every direction. Olsson and Bolin (2014) on the other hand, developed a model that accounts for central place foraging behaviour, which states that a resource patch is not worth foraging if the foraging costs equate to the collected resource value. They demonstrated how the model can be used for white storks (*Ciconia ciconia*), while Nicholson et al. (2019) compared and validated the Olsson and Bolin (2014) model and the Lonsdorf et al. (2009) model in predictions of social and solitary bee visitation in *Vaccinium corymbosum* L. (highbush blueberry) crops in agricultural landscapes in the USA. The Lonsdorf et al. (2009) model predictions did not fit bee observation data from the field when comparing bee visitation data between open scrub habitat and blueberry crops, while the Olsson and Bolin (2014) model predictions did (Nicholson et al., 2019). This outcome indicated that the central place foraging theory better represents real-life observations than simply assuming foraging probability decreases with distance from a nest.

Häussler et al. (2017) went a step further by incorporating into their spatially-explicit model, in addition to central place foraging behaviour, a consideration of bee population growth as well as two flight distance options; one for dispersing queens and one for foragers. Model outputs for each landscape included quantity of new bumblebee queens that go on to hibernate, bumblebee colony size (average workers/colony) and the quantity of colonies (per hectare). Pollination outputs included, among others, the mean rate of bumblebee visits to *Brassica napus* L. (visit rate/ha). Häussler et al. (2017) ran simulations of the model for 35 years for 20 different landscapes in Sweden, along gradients of increasing cover of *B. napus* L. and heterogeneity of the landscape. Simulations were based on the behaviour of a typical early-emerging bumblebee species. The effect of adding different management interventions (e.g. flower strips), designed to enhance the resources available to pollinators were also simulated (Häussler et al., 2017). Bumblebee colony growth, the number of colonies and, the number of new queens produced at the end of the foraging season were all greater in the simulations when compared to a baseline simulation with no additional interventions, as was the pollination of *B. napus* (Häussler et al., 2017).

Gardner et al. (2020) validate the Häussler et al. (2017) model by comparing wild bee abundance data to model predictions. Data from 239 British sites were used. The model was used to generate visitation rate (per m^2) predictions for four pollinator guilds (cavityand ground-nesting solitary bees and tree- and ground-nesting bumblebees), for the area surveyed on the ground. These predictions were then compared to the ground-survey data using a linear model. Expert opinion (e.g. for scoring land cover classes according to the floral resources that they provide as well as the nesting and floral attractiveness of each class) and literature sources (e.g. maximum nest density; Häussler et al., 2017) are used to allocate model parameter values. Using initial expert-derived scores, model and ground-truth data demonstrated significant agreement for each guild, although this was not linear. Separately, model calibration was carried out using a sub-set of the sites (see Gardner et al., 2020 for full calibration details) and two alternative methods: the first including all parameters at the same time and the second prioritising parameter calibration based on the outcome of a sensitivity analysis that identified parameters that were particularly influential in the model. Calibration improved the linear model fit (R^2) between modelled and ground data for each guild apart from tree-nesting bumblebees when using the second calibration technique that involved prioritising parameters.

Remaining limitations of each of the aforementioned models (Gardner et al., 2020; Häussler et al., 2017; Lonsdorf et al., 2009) include the fact that they do not allow the incorporation of within or between-species competition for resources (Häussler et al., 2017; Nicholson et al., 2019). Neither do they allow the incorporation of other stressors into the model or any estimate of accessibility of floral resources, e.g. whether tongue length allows a particular bee species to access the nectar from a particular flower species. An alternative to the process-led models described above are agent-based models (Gardner et al., 2020). Agent-based models that can assess growth and survival at the colony level in social bee species have been developed (Becher et al., 2014; Becher et al., 2018; Twiston-Davies et al., 2021). The Bumble-BEEHAVE model for example, incorporates spatially-explicit data on the availability of nectar/pollen resources within a landscape, to allow simulations of bumblebee dynamics from the individual to the landscape level (Becher et al., 2018). Bumblebee behaviour (e.g. according to their caste), physiology (e.g. tongue length) phenology (e.g. time at which queens emerge from hibernation) are all taken into account, as is the availability and accessibility of individual flowering plant species and the foraging resources (nectar/pollen) that they provide (Becher et al., 2018). Unlike the aforementioned process-based models, the Bumble-

BEEHAVE model also allows for the incorporation of stressors (e.g. badger predation, weather conditions or exposure to pesticides).

Becher et al. (2018) compare bumblebee data on the ground, obtained from the literature, to model simulations. At the population-level for example, *Bombus terrestris* nest densities as simulated through the model (34.0 nests/km^2) were found to be similar to the average nest density estimated on the ground (28.7 nests/km^2) by Knight et al. (2005). However, Becher et al. (2018) were unable to carry out exact model calibration, as underlying variable data shaping the bumblebee data on the ground were not available. A major disadvantage of agent-based approaches such the Bumble-BEEHAVE model is that they are computationally very intensive (Gardner et al., 2020). The Bumble-BEEHAVE model is also currently limited to modelling the dynamics of six bumblebee species commonly found in the UK (Becher et al., 2018).

A key limitation of spatially-explicit modelling approaches or tools, is that they currently rely on estimates of floral and nesting resources for a particular land cover category/habitat type. Estimates are often empirically calculated using quadrat surveys and then scaled up to the habitat level, derived through expert opinion or, are based on evidence within the scientific literature (e.g. Becher et al., 2018; Gardner et al., 2020; Häussler et al., 2017; Lonsdorf et al., 2009; Nicholson et al., 2019). As an alternative, very-high resolution remotely-sensed imagery could potentially be used to classify and map the actual fine-scale spatial distribution of the floral component of different flowering plant species (Henrys and Jarvis, 2019), therefore providing an exact floral cover estimate for each flowering plant species within each model cell. Based on classifications outlining the spatial distribution of different flowering plant species, estimates as to the spatial distribution of floral resources such as pollen or nectar could also be made. Estimates derived through spatially-explicit models, of different pollinator metrics within an agricultural landscape and/or the pollination services provided to nearby crops, could subsequently be refined based on a more accurate representation of pollinator forage species on the ground.

1.9 Thesis aims and structure

I address two key aims in this PhD thesis. The first is to determine whether the nectar resource can be mapped using high-resolution remote-sensing technology. The second is to assess whether pollinator abundance is related to the fine-scale within-habitat variability of the nectar resource. These aims are addressed and discussed in the following four Chapters. An overview of the thesis structure can be seen in Figure 1.1 and Figure 1.2 and an overview of the study area can be found in Figure 1.3 and Figure 1.4.

1.9.1 Chapter 2

The nectar sugar resource is usually estimated using on-the-ground quadrat surveys. However, these can be time and labour-consuming and only provide an estimate of the floral resource density by taking an average density across quadrats, rather than measuring the true distribution and variability in density (Barnas et al., 2019; Willcox et al., 2018). Remote-sensing surveys provide an alternative surveying method that could directly measure the spatial distribution of floral resources over large areas (for example all margins across a farm) in a relatively-short time-frame. This would be subject to having a high classification accuracy. In Chapter 2, I determine whether high-resolution remotely-sensed multispectral airborne imagery has the potential to accurately classify the floral component of nectar-rich flowering plant species within a UK arable farming context. I use a parametric maximum likelihood classifier to achieve this aim. I focus on nectar-rich flowering plant species found within hedgerows and sown field margins, as these habitat types are known to be two of the most important sources of nectar within UK arable landscapes (Baude et al., 2016; Timberlake et al., 2019). I ask:

1.) Can multispectral airborne imagery with spatial resolutions of 3cm and 7cm be used to accurately classify five nectar-rich flowering plant species within hedgerow and wildflower margins?

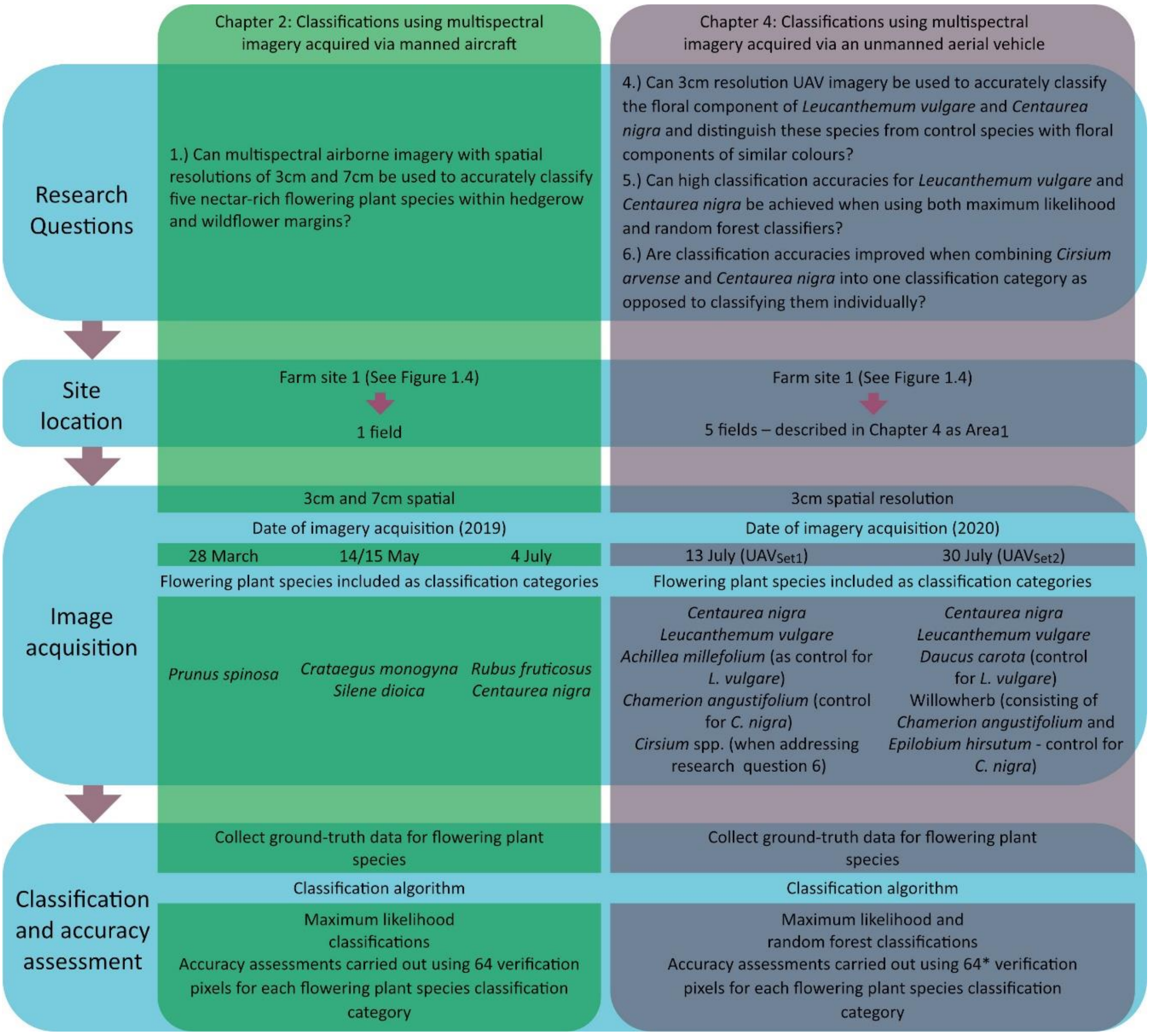


Figure 1.1 A flow-chart outlining the remotely-sensed imagery acquisition and classification carried out in this thesis in Chapters 2 and 4. Note that the research questions are numbered according to their order in the thesis. *Note that 64 verification pixels were used for the majority of classification accuracy assessments, although only 53 pixels were used for *Leucanthemum vulgare* for some of the accuracy assessments. See Chapter 4 for more detail.

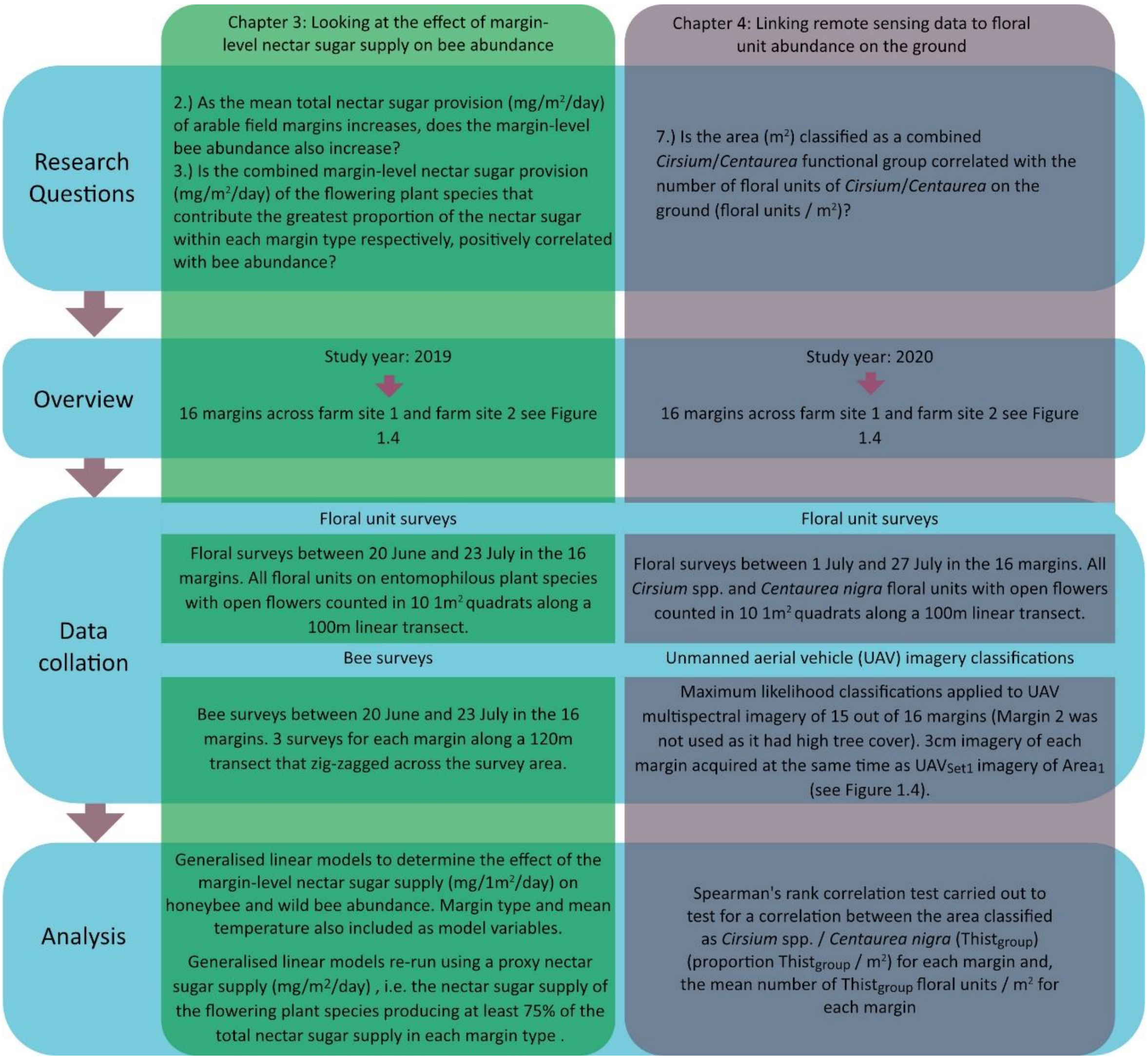


Figure 1.2 A flow-chart outlining the structure of the thesis in addressing the research questions focused on the effect of within-habitat nectar sugar supply on bee abundance and the link between on-the-ground floral resources and remote-sensing.

Figure 1.3 The location of study site relative to the United Kingdom (Google Earth Pro V 7.3.4.8642, 2015)

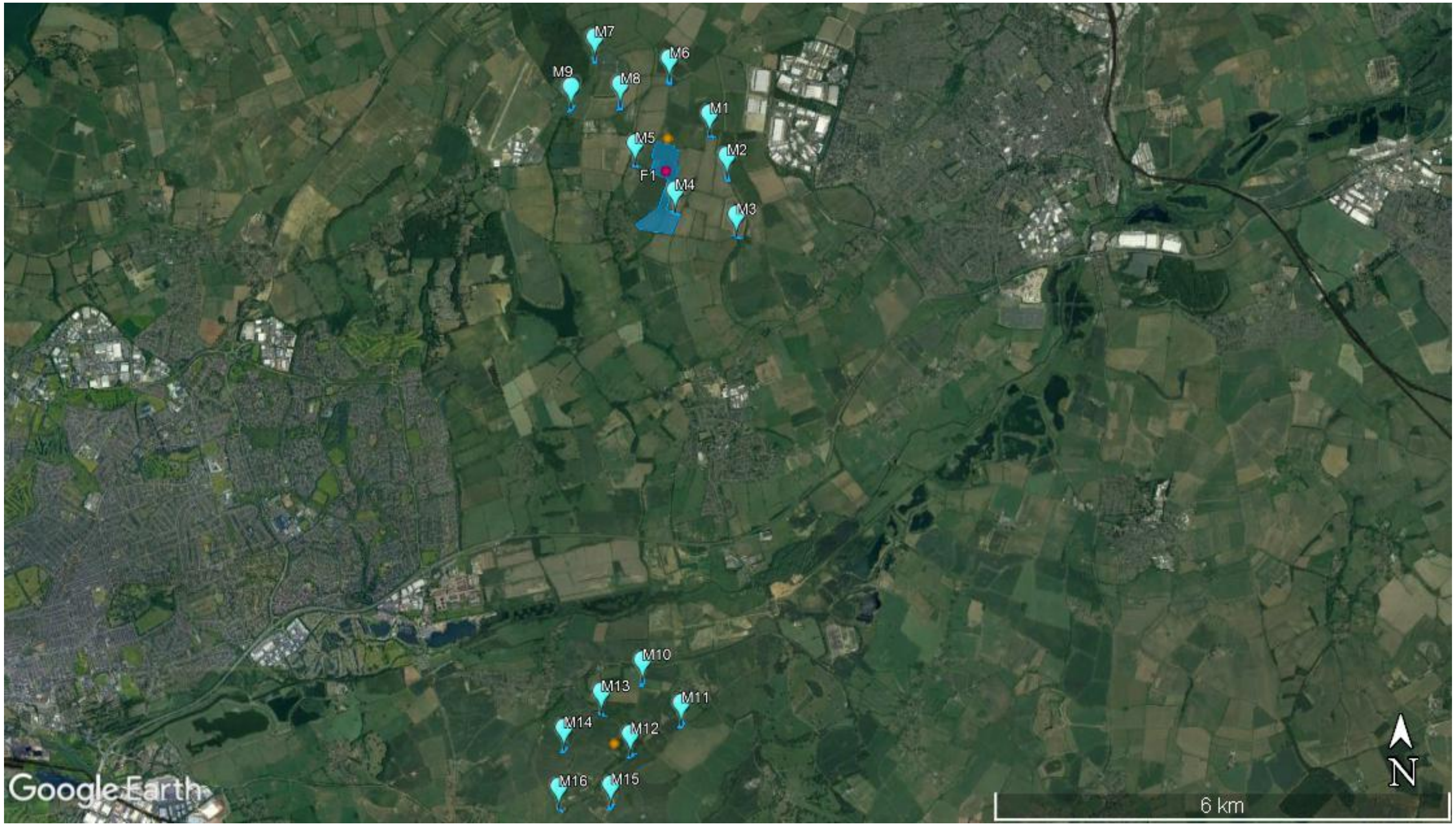


Figure 1.4 The location of Area$_1$ (blue polygon) in Chapter 4, each of the 16 margins in Chapters 3 and 4 (labelled M1 to M16) and Field 1 (labelled as F1) in Area$_1$ which is the study field for Chapter 2. The orange points show the approximate location of the centre of each farm site and are ~7.98km apart.

(Google Earth Pro V 7.3.4.8642, 2020a)

1.9.2 Chapter 3

As reviewed in Section 1.4, studies have focused upon the relationship between nectar sugar availability and pollinator communities at a national (Baude et al., 2016) or farm/landscape level (Langlois et al., 2020; Timberlake et al., 2021). However, this does not capture the within-habitat fine-scale variability in nectar sugar supply and its relationship with pollinator metrics. Hicks et al. (2016) assessed the differences in nectar sugar provision between different sown flower mixes in an urban context, but did not relate this data to any pollinator metrics. As far as I am aware, no studies have focused on the nectar sugar supply within arable field margins and related this to pollinator abundance. This is the main focus of Chapter 3, where I model the margin-level bee abundance as a function of the nectar sugar availability and two margin types (naturally regenerated and sown with a wildflower mix) using generalised linear models. I also ask whether the nectar sugar supply of the flowering plant species producing the greatest proportion of the total nectar sugar within arable field margins can be used as proxies for total nectar availability in the bee abundance models. Specifically I ask:

2.) As the mean total nectar sugar provision (mg/m^2/day) of arable field margins increases, does the margin-level bee abundance also increase?

3.) Is the combined margin-level nectar sugar provision (mg/m^2/day) of the flowering plant species that contribute the greatest proportion of the nectar sugar within each margin type respectively, positively correlated with bee abundance?

1.9.3 Chapter 4

In Chapter 4, I expand upon the remote-sensing foundation constructed in Chapter 2. I determine whether Unmanned Aerial Vehicles are suitable platforms for acquiring imagery and classifying the floral component of nectar-rich flowering plant species. I refine the ground-truth methods used in Chapter 2 and apply them to additional flowering plant species with synchronously flowering control species. I classify imagery using both Maximum Likelihood and Random Forest classifiers to determine whether one classifier is better suited to mapping the species of interest. Finally, I consider how classification outputs are related to the actual floral resource on the ground. I ask:

4.) Can 3cm resolution UAV imagery be used to accurately classify the floral component of *Leucanthemum vulgare* and *Centaurea nigra* and distinguish these species from control species with floral components of similar colours?

5.) Can high classification accuracies for *Leucanthemum vulgare* and *Centaurea nigra* be achieved when using both maximum likelihood and random forest classifiers?

6.) Are classification accuracies improved when combining *Cirsium arvense* and *Centaurea nigra* into one classification category as opposed to classifying them individually?

7.) Is the area (m^2) classified as a combined *Cirsium*/*Centaurea* functional group correlated with the number of floral units of *Cirsium*/*Centaurea* on the ground (floral units / m^2)?

1.9.4 Chapter 5

In Chapter 5, I consider the next steps for the research presented throughout this PhD thesis. I consider for example, in a UK agricultural context, which nectar-rich flowering plant species should be considered for inclusion in a remote sensing programme for estimating the nectar sugar resource available to pollinators. I also consider alternative options, should some nectar-rich flowering plant species remain spectrally inseparable from one another. The various remote sensing techniques that I describe are tested and validated at a single farm location. I therefore consider how the research can be scaled up and applied across multiple farming systems in the UK, for example with varying environmental conditions, such as soil type. Finally, I consider how the research and remote sensing methods developed can be applied in a practical sense by agricultural and conservation practitioners, to facilitate resource management for pollinators in intensively farmed arable systems.

Chapter 2

Mapping nectar-rich pollinator floral resources using airborne multispectral imagery

2.1 Introduction

2.1.1 Meeting pollinator resource requirements

As discussed in Chapter 1, land-use changes linked to the intensification of agricultural activities are key contributors to pollinator decline (Goulson et al., 2015; Potts et al., 2010; Potts et al., 2016). Both the Netherlands and UK have experienced reductions in bee species richness (Biesmeijer et al., 2006; Carvalheiro et al., 2013; Powney et al., 2019). Both countries also have highly altered habitats. Baude et al. (2016) discovered that pollinator decline patterns in Britain mirrored reductions in nectar sugar supply and diversity. This study and others (e.g. Carvell et al., 2017; Pywell et al., 2005; Scheper et al., 2013), suggest that increasing the availability and variety of nectar-rich flowering plant species could go a long way in addressing pollinator losses.

Arable habitat produces the least nectar out of all of Britain's habitat types as well as the least variety (Baude et al., 2016). Increasing and better managing existing pollinator foraging resources alongside crops, could therefore contribute greatly to conservation efforts.

Positive relationships have long been established between broad landscape level vegetation categories and pollinator or crop-visitor population metrics, such as species richness and abundance (Pywell et al., 2005; Scheper et al., 2013; Willcox et al., 2018; Kleijn et al., 2015; Ricketts et al., 2008). However, knowledge surrounding the specific within-habitat variables contributing to these relationships, such as availability of nesting sites or nectar/pollen supply, remains limited (Willcox et al., 2018). Some studies have started to address this (e.g. see Holl et al., 1995; Timberlake et al., 2021). Precise estimates of how resources such as pollen and nectar vary temporally and at different spatial scales are essential for understanding the numbers of pollinators that can be supported at a landscape level (Carl et al., 2017; Timberlake et al., 2019).

2.1.2 Remote sensing for mapping pollinator resources

Field surveying of floral/vegetation resources to gather information at finer scales is usually time and space limited. Often, only a subset of floral resources can be mapped and subsequently used to estimate resources available at the wider habitat or landscape level (Baude et al., 2016; Pettorelli et al., 2018b; Timberlake et al., 2019). Remote sensing has enormous potential to facilitate the fine-detailed mapping of pollinator resources and fill in research gaps (e.g. see Galbraith et al., 2015; Willcox et al., 2018). Chapter 1 outlined studies where pollinator researchers have started taking advantage of these remote sensing opportunities (Galbraith et al., 2015; Gardner et al., 2020; Willcox et al., 2018). Carrié et al. (2018) for example, used multispectral satellite imagery with a 2m pixel size to determine the relationship between nesting resource metrics in permanent grassland habitats and the bee communities in crop fields. Xavier et al. (2018) developed a technique using Unmanned Aerial Vehicle (UAV) imagery with a pixel resolution of 1cm to capture the floral resource within experimental plots. They produced classification outputs with three categories: bare ground, flowers and other vegetation. Pollinator visits were found to positively correlate both with field survey flower counts and floral area as obtained from these classification outputs (p-values of <0.001 and 0.0007 respectively).

While not focusing specifically on pollinator ecology, Bradter et al. (2020) used airborne hyperspectral imagery and simulated multispectral data with a 1m pixel resolution, to classify farmland grassland habitats into distinct vegetation categories. Vegetation categories were grouped according to dominant plant species or British National Vegetation classification categories. Other studies have demonstrated that flowers of individual plant species can be detected using remote sensing. Chen et al. (2009) demonstrate that hyperspectral data acquired with a spectroradiometer can be used to estimate the floral cover of *Halerpestes tricuspis* within a Tibetan grassland context. Carl et al. (2017) achieved an overall accuracy of 99.5% when using ImageJ to distinguish between invasive *Robinia pseudoacacia* L. flower and vegetation biomass pixels within red-green-blue UAV imagery. Horton et al. (2017) created a peach blossom detection algorithm in MATLAB which they used to detect peach blossom pixels with an 84.3% success rate using multispectral UAV imagery. Nonetheless, there remain very few studies globally that focus specifically on mapping floral resources (Landmann et al., 2018).

Important pollinator food resources often constitute very small-scale plants, for example, grassland species such as *Centurea nigra* and *Leucanthemum vulgare* (Baude et al., 2016). Many of these species are also included within commercial pollinator-friendly field margin mixes (Emorsgate Seeds, 2021). Being able to quantify the availability of these flowering plant species is important because they differ widely in their provision of the key floral resources, nectar and pollen (Baude et al. 2016). For example, for those UK species with empirical nectar data available, flow rates per flower vary by three orders of magnitude, ranging from 0 - 7667.84 µg sucrose/flower/day (Baude et al., 2015a). Flowering plant species also differ in their ability to provide floral resources to different pollinator species or functional groups (e.g. Dicks et al., 2015, Table S1). None of the aforementioned studies determined whether the floral units (defined by Carvell et al., 2007; see methods) of individual flowering plant species within arable field margins can be accurately classified and mapped using very high spatial resolution remotely sensed data.

Similarly, flowering hedgerow species provide an important food resource to pollinators within farmed landscapes (Baude et al., 2016; Garratt et al., 2017; Häussler et al., 2017; Timberlake et al., 2019). While hedgerow locations within a landscape have been successfully mapped (Betbeder et al., 2015; Tansey et al., 2009; Vannier and Hubert-Moy, 2008; Vannier et al., 2011), to my knowledge, flowering plant species within a northern European hedgerow context have not.

This study focuses on species found within UK agricultural field margins and hedgerows, because of the high potential value of these habitat types for pollinators (Baude et al., 2016; Timberlake et al., 2019; Häussler et al., 2017). I determine whether the floral units of three hedgerow species (*Prunus spinosa*, *Crataegus monogyna* and *Rubus fruticosus*) and two arable margin species (*Silene dioica* and *Centaurea nigra*) can be classified and mapped using multispectral airborne imagery and a maximum likelihood classifier.

2.1.3 Choice of classifier and spatial resolution

A maximum likelihood (ML) classifier was chosen due to the fact that I was working in collaboration with an industry partner H L Hutchinsons Ltd. (Hutchinsons, 2021a), who were interested in the development of a remote sensing method that could relatively cheaply and easily be used on the ground. The ML classifier meets these requirements and is readily available through multiple software packages (Lu and Weng, 2007). This parametric classification approach relies on the distribution of pixel values within data bands. Based on this distribution, the ML classifier then allocates each pixel to the classification category that it is most likely to belong to (Lillesand et al., 2015). More recently, much remote sensing research has turned to machine-learning classifiers such as random forest. However, at the time of my research most software packages that offered random forest either had a substantial cost involved (e.g. eCognition) or required a detailed knowledge of coding (e.g. the 'randomForest' package in R) rather than an easy to use graphical-user-interface (Belgiu and Drăguţ, 2016). The latter would make random forest an impractical classifier for use within agricultural operations. These challenges influenced my choice to use an ML classification algorithm, which have been successfully used for many ecological remote sensing applications such as the mapping of wetlands (Guo et al., 2017) or the production of maps of land use/land cover change (Islam et al., 2018).

Choice of imagery spatial resolution was another important consideration for this study. Too high a spatial resolution can lead to greater within-class spectral variability and a greater chance of spectral signature overlap between differing features (Pu et al., 2011; Gong & Howarth, 1990; Latty et al., 1985; Toll, 1985). On the other hand, too low a spatial resolution in the context of individual floral units could lead to a greater chance of mixed pixels which could also lead to reduced classification accuracies for individual flowering plant species (Foody & Arora, 1996; Shanmugam et al., 2006). As the floral unit width of the flowering plant species of interest ranged between 1-3cm (NatureGate, 2020), I chose a pixel width of 3cm as a starting point. However, the standard pixel size used by many farmers for crop monitoring in the UK is 7cm. As a 7cm spatial resolution is widely utilised and is considerably cheaper than a 3cm resolution, I also investigated whether a 7cm pixel size could be used to classify the flowering plant species of interest.

Specifically, I address the following research question:

1.) Can multispectral airborne imagery with spatial resolutions of 3cm and 7cm be used to accurately classify nectar-rich floral resources within hedgerow and wildflower margins?

2.2 Materials and Methods

2.2.1 Study site and target nectar-rich flowering plant species

A conventional arable farm in Northamptonshire, UK was chosen as the study location (52°17’57”N, 0°45’49”W). The farm was 809 ha in size and the predominant crops were wheat, barley and oilseed rape. One field was used as the study site (Figure 2.1). Two sides of the field were sown with margins that had been planted with the EM1 pollinator wildflower mix from a UK-based wildflower seed provider: Emorsgate seeds (Emorsgate Seeds, 2021). The full list of species included as part of the mix can be found in Appendix 2.1. Some species not included in the mix were also growing within the EM1 margins, such as *Trifolium repens*. The field was also surrounded on two sides by hedgerow containing *Prunus spinosa* and *Crataegus monogyna* and on a third side by thick *Rubus fruticosus* scrub.

When deciding upon target margin flowering plant species, these had to be distributed across several margin subsections and flowering abundantly enough within margins to provide adequate ground-truth data for the classification stage. Following Fisher et al. (2018), I considered a minimum of 100 pixels of data to provide adequate ground-truth data (see Section 2.2.3 for further detail). Out of the flowering plant species that met this criterion, for each image acquisition date (28th March, 14th/15th May and 4th July 2019) I selected the species within the EM1 wildflower mix that produced the greatest quantity of nectar per floral unit according to data from Baude et al. (2015a) and Baude et al. (2015b). I used the definition of Carvell et al. (2007) for floral units: either individual flowers or stems with multiple flowers that a bee can walk rather than fly between, e.g. one *C. nigra* capitulum. *Silene dioica* was therefore selected as the target margin flowering plant species for May and *Centaurea nigra* as the target flowering plant species for July (see Table 2.1). No margin species were flowering in March.

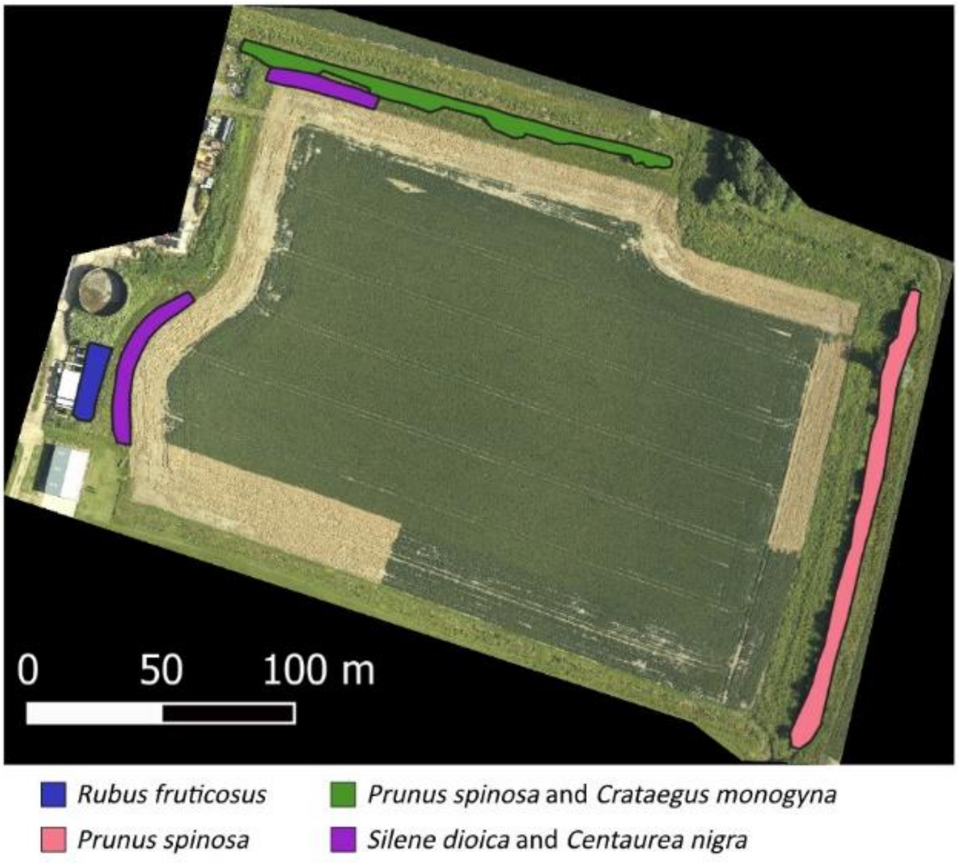


Figure 2.1 The study field with the areas used for selecting training and verification pixels for each flowering plant species highlighted. See Figure 1.4 in Chapter 1 for the location of this field in the context of the wider study area.

There were fewer nectar-rich flowering plant species within hedgerows. Subsequently, hedgerow species were included as target species in this study if they were flowering abundantly enough to generate adequate ground-truth data for the classification stage (i.e. at least 100 pixels of data covering several hedgerow subsections or a hedgerow section of greater than 3m). The target species were subsequently *Prunus spinosa* flowering in March, *Crataegus monogyna* flowering in May and *Rubus fruticosus* flowering in July (Table 2.1).

Table 2.1 Target nectar-rich flowering plant species for which field data were gathered, their nectar production values and approximate floral unit size

Date of image acquisition	Dates gathered ground-truth data	Location (margin / hedgerow)	Flowering plant species (common name)	Nectar sucrose secretion rate per floral unit per day (µg)[1]	Approximate floral unit[2] width (cm)
28 March	NA	Hedgerow	*Prunus spinosa* (blackthorn)	266.23	1.0-1.8[3]
14/15 May	NA	Hedgerow	*Crataegus monogyna* (hawthorn)	102.47	1.0[3]
14/15 May	15-18 May	Margin	*Silene dioica* (red campion)	450.65	2.0-3.0[3]
4 July	04-11 July	Margin	*Centaurea nigra* (common knapweed)	10705.66	2.4 (0.9)[4]
4 July	NA	Hedgerow	*Rubus fruticosus* (bramble)	1892.83	1.9 (0.1)[4]

[1]Mean nectar sucrose per flower from Baude et al. (2015a) multiplied by mean no. flowers per floral unit from Baude et al. (2015b).

[2]Note that the term floral 'unit' in the table uses the definition of Carvell et al. (2007) whereby any flower or stem with multiple flowers that a bee can walk rather than fly between constitutes one unit.

[3]Values from NatureGate (2020) and only an approximate value.

[4]The values for *Centaurea nigra* and *Rubus fruticosus* are my mean measurements obtained in 2020 (see Appendix 2.2). Variance is reported in the brackets.

2.2.2 Acquisition and processing of aerial imagery

Remotely sensed aerial imagery was acquired using two Hasselblad A6D-100c (50mm) cameras attached with bayer filters, on 28th March, 14th/15th May and 4th July 2019 by Spectrum Aviation. The sensors were mounted on a Sky Arrow 650 manned aircraft. Two sets of data with spatial resolutions of approximately 3cm and 7cm were obtained for each month. Data acquisition flights were only launched on days that were forecast to be cloud-free (no more than 1/8 cloud coverage, with visibility greater than 10km) and with low wind (<20kts).

Spectrum Aviation carried out the initial pre-processing. Agisoft Metashape (Agisoft, 2019) was used to tie the images together. Data were processed under a WGS 84 (EPSG: 4326) coordinate reference system (CRS). However, the final 6-band orthomosaics for each month and resolution were exported for use within classifications under an OSGB 1936 / British National Grid (EPSG: 27700) CRS.

I imported the final 6-band 16bit orthomosaic images for each month into QGIS version 3.4.15 (QGIS, 2020) and split the stacked images into their component bands. Three of the six bands were acquired using a dual filter. They each contained a combination of red and near-infrared (NIR) wavelengths and only the one which had the highest proportion of NIR was kept, along with the red-green-blue (RGB) bands. Each band was 15nm wide. The RGB and NIR bands were stacked back together into a 4-band image for each month which was used in the classification process. As I was interested in whether aerial imagery could accurately map high nectar-producing floral resources at a single point in time, I did not convert from digital number values to reflectance, following Xavier et al. (2018).

2.2.3 Gathering ground-truth data for margin species

Ground-truth data were collected within eight days of each image acquisition date (Table 321). For the margin species, ground-truth data were gathered for individual remote sensing (RS) units. For *Centaurea nigra*, RS units were defined in the same way as floral units following Carvell et al. (2007), i.e. one capitulum constituted an RS unit (Figure 2.2a). Such an approach was not possible for *Silene dioica* because for this species floral units as defined by Carvell et al. (2007) are individual flowers. For remote sensing purposes, any *S. dioica* flowers on the same main stalk were counted as a single RS unit, because they would be likely to occur within the same pixel space in the aerial images (Figure 2.2b, c).

Figure 2.2 a. One *Centaurea nigra* capitulum constitutes a remote sensing unit **b.** One *Silene dioica* remote sensing unit with multiple flowers **c.** A second *S. dioica* remote sensing unit with only one flower.

Location data were gathered for 85 *S. dioica* RS units and 100 *C. nigra* RS units. RS units for each species were purposively selected based on how they were spread across the margins (see Appendix 2.3).

Two techniques were used to accurately measure the location of individual RS units. Distances to at least two ground-control points (GCPs) were measured on the ground using a DeWALT laser beam measure (±1.5mm) (following Xavier et al., 2018; see Appendix 2.4). In addition, for a subset of RS units I gathered waypoint locations using a Topcon Real-time Kinetic (RTK) HiPer V receiver (Topcon, 2020).

2.2.4 Locating flowering plant species within the imagery

The accuracy of the RTK receiver was tested by recording waypoints at the corners of a ground-control point board. As the waypoints were not located in the correct position in the imagery, the RTK receiver was found to be an inaccurate means of locating *Silene dioica* and *Centaurea nigra* remote sensing (RS) units in May and July imagery respectively. I subsequently only used RS unit location data obtained via our method of measuring the distance of RS units to known ground-control points (GCPs).

Even when measuring the distance of RS units to known GCPs, there was no way of determining exactly what error was involved in the ground location measurements relative to the imagery. For example, gusts of wind could change RS unit locations at the exact moment that an image was acquired. I was consequently unable to precisely locate individual RS units within the imagery. However, data had been gathered for multiple RS units within clusters of floral units of *S. dioica* and *C. nigra* (Appendix 2.3). I also knew that non-target flowering plant species with potentially similar spectral signatures within the visible range were either not flowering synchronously with *S. dioica* or *C. nigra* or, they were located in different parts of the margin. For example, *Cirsium arvense* was flowering synchronously to *C. nigra*, but *C. arvense* floral units were at the very least several metres away from the *C. nigra* RS units that were used in the ground-truth process. I therefore combined the ground-truth data and knowledge of the surrounding area with the fact that *S. dioica* and *C. nigra* are both distinct pink/purple in colour. The assumption was made that any purple pixels within close proximity to the predicted RS unit locations belonged to clusters of *S. dioica* or *C. nigra* in May and July imagery respectively. Classification training and verification pixels were selected from within these floral clusters (Figure 2.3). If, despite the predicted locations of RS units, pink/purple pixels could not be located in the vicinity, I did not use these areas within classification training and verification processes.

For hedgerows, none of the target flowering hedgerow species flowered synchronously. *Prunus spinosa,* flowering during acquisition of the March image, had finished flowering by May when the second image was acquired and during which time *Crataegus monogyna* was flowering. Similarly, *C. monogyna* had finished flowering by the time of the July image acquisition, during which time *Rubus fruticosus* was flowering. As the floral units of each of these species are white or almost white and flower in dense clusters often several metres long or more, any white floral unit pixels within imagery from each acquisition date could safely be allocated to the appropriate species (see Figure 2.4).

Figure 2.3 Measured locations of individual *Centaurea nigra* remote sensing (RS) units within 3cm imagery (pale blue points). These multiple RS unit locations outline an area of flowering *C. nigra* which given the knowledge of the surrounding margin area, meant I assumed that any purple pixels within close proximity to the predicted RS unit locations belonged to *C. nigra*. The area from which purple pixels were selected as *C. nigra* for inclusion within the training layer is circled in dark blue. There is no certainty that each point falls exactly on top of an RS unit in the image.

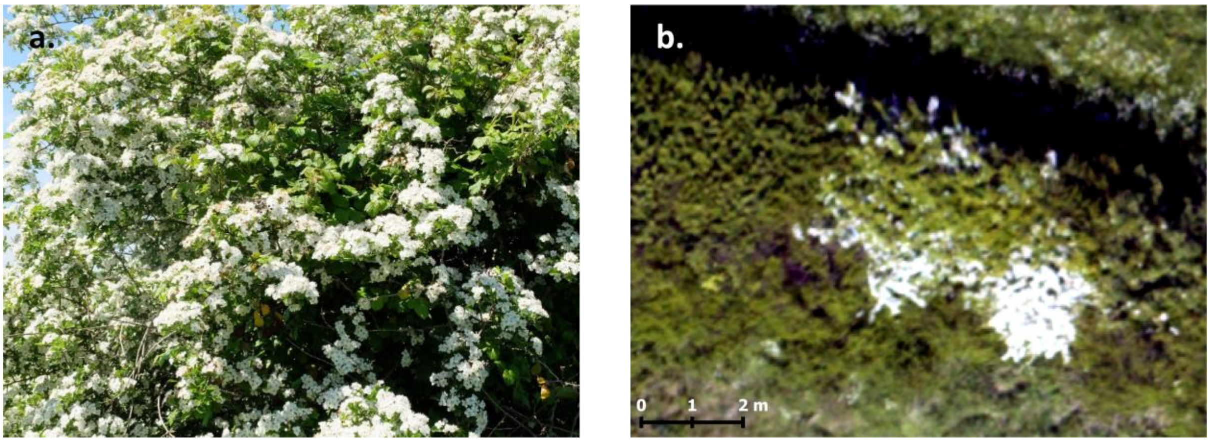


Figure 2.4 a. An image of a patch of *Crataegus monogyna* taken from the ground and b. A sub-section of the multispectral image for May (3cm resolution) showing a patch of flowering *Crataegus monogyna*.

2.2.5 Image training and classification

The semi-automatic classification (SCP) plugin (Congedo, 2016) in QGIS version 3.4.15 (QGIS, 2020) was used for training a maximum likelihood classifier and running the classification. This platform was chosen as it is open source and has all classification and accuracy assessment tools within one easy-to-use graphical user interface.

I started by training and classifying the 3cm images for each month. Each target flowering plant species formed a classification category within the classifications for the respective months in which they were flowering. For each month an 'other' classification category was also created. This contained all features within the imagery that I was not interested in classifying individually, such as green vegetation, soil or branches.

Training data were gathered for each flowering plant species classification category by selecting pixels within the imagery known to belong to that species based on ground-truth data. A 'seed' pixel was initially selected and then a region growing tool was used to select other pixels within a threshold distance. In this way I ended up with groups of pixels at different training locations for each species, each with a spectral signature showing the mean digital number values in each band for that pixel group. I repeated the process for the 'other' classification category, making sure to select seed pixels across a range of different features so that I ended up with many sub-categories all contained under the main 'other' classification category. The classifications were later run at the level of this main 'other' category, e.g. if the algorithm allocated a pixel to a 'green vegetation' sub-category, this would appear as belonging to the 'other' classification category in the classification output raster.

Pixels on the edge of clusters of floral units may contain other features as well, e.g. another flowering plant species or grass, which could affect the spectral signature within those edge pixels. Both 'pure' and 'edge' seed pixels were therefore chosen to cover spectral variability when gathering training data. The former were the whitest/pinkest pixels (depending on flowering plant species) in the centre of patches. The latter were those pixels that were either on the edge of patches or, were in the centre of a very small patch and appeared to be mixed with other vegetative features. Table 2.2 below provides the total number of training pixels for each classification category for each month.

Maximum likelihood classification algorithms were applied to the 3cm imagery for each month using the training sets for each month respectively. Several training set iterations were applied to determine the influence upon classification accuracy, e.g. by including or excluding edge region training data.

'Edge' refers to pixels either on the edge of patches or, in the centre of a small patch and mixed with other vegetative features.

Spectral signatures for pixel groups created by the region growing tool within a particular classification category could be merged together to provide a mean spectral signature for the whole classification category, e.g. a merged signature for *Silene dioica*. If spectral signatures between different classification categories overlapped slightly, pixel groups could be removed from a classification category to change its mean spectral signature. This was a way of manually changing thresholds within a classification training set so that an image pixel would be allocated to one classification category over another.

Atmospheric conditions could potentially vary between the acquisition of 3cm and 7cm data for each month. However, as the target flowering plant species were very distinct colours, I hypothesised that 3cm training data could also be used to classify 7cm imagery (Dash et al., 2019). I therefore used training data collated for each month using 3cm imagery to classify the 7cm imagery for each month respectively. Only the training set iterations that resulted in the best classification accuracies for each month for 3cm imagery were applied to the 7cm imagery for each month.

I also verified whether 7cm data was a high enough resolution to train a classification and achieve high classification accuracies. A training set was subsequently created using May 7cm imagery, keeping the training pixel locations as similar as possible to those within the 3cm imagery training set. The May 7cm image was then classified using this new training set.

Table 2.2 Number of training pixels per classification category for classification iterations for each month

Imagery month	Classification category	Merged classification sub-category	Total number of training pixels	Classification iteration in which pixels were included
March	*Prunus spinosa*	Pure pixels	120	1, 2
	Prunus spinosa	Edge pixels	57	1
	Other	Various sub-categories	11919	All
May	*Silene dioca*	Edge pixels (merged)	18	3
	Silene dioca	Pinkest pixels (non-merged)	62	1, 4
	Silene dioca	Pinkest pixels (merged)	5	2, 3
	Crataegus monogyna	Centre pixels (merged)	44	1, 2, 3
	Crataegus monogyna	Centre pixels (non-merged)	91	4
	Other	Various sub-categories	11193	All
July	*Rubus frutisosus*	Pure pixels (merged)	94	1, 2, 3, 4, 5, 6, 7, 8
	Rubus frutisosus	Edge pixels (merged)	97	1, 2, 3, 4, 5, 6, 7
	Centaurea nigra	Pure group a to a4 (merged)	27	3, 4, 5
	Centaurea nigra	Edge pixels (merged)	8	1, 3
	Centaurea nigra	Edge 'high' signature (merged)	5	5

Centaurea nigra	Edge 'lower' signature (merged)	8	5
Centaurea nigra	Edge 'middle' signature (merged)	7	5
Centaurea nigra	Pure (merged)	30	1, 2, 8
Centaurea nigra	Pure (non-merged)	30	6
Centaurea nigra	Pure group a to a4 (non-merged)	27	7
Other	Various sub-categories	5747	All

Note: 'Pure' refers to the whitest/pinkest pixels (depending on flowering plant species) in the centre of patches.

2.2.6 Accuracy assessment

An independent accuracy assessment for each classification was carried out using error matrices, through which overall accuracy, user's accuracy and producer's accuracy metrics were calculated (as in Sankey et al., 2018; Schmidt et al., 2018). A kappa statistic was also calculated (Lillesand et al., 2015). The number of verification pixels used for each classification category can be found in Table 2.3. Full accuracy assessment methods and error matrices are provided in Appendix 2.5 and Supplementary Data 1-2 respectively.

Verification pixels included in the accuracy assessments were all at least 0.2m away from pixels included within the training set or were very obviously in a different land-cover category, e.g. a training pixel clearly located in a section of gravel and the verification pixel clearly located in a section of grass. Given that imagery had only a 3cm or 7cm spatial resolution, 0.2m was considered a sufficient distance to provide independence between training and accuracy data sets.

2.3 Results

2.3.1 Overall accuracy and kappa statistics

Error matrices constructed for each 3cm resolution classification can be found in Supplementary Data 1 (digitally accompanying the thesis) Error matrices constructed for classifications carried out on 7cm imagery can be found in Supplementary Data 2 (digitally accompanying the thesis). Note that only the classification training set iteration for each month that achieved the greatest overall accuracy for 3cm data was used for classifying the respective 7cm imagery. The classification iterations for each month and at each resolution that achieved the best overall classification accuracy are outlined in Table 2.4 along with their respective kappa statistic values.

Table 2.3 Number of verification pixels for each classification category included in the accuracy assessments for each month

Month of data acquisition	Classification category	Number of verification pixels included in accuracy assessment	
		3cm classifications	7cm classifications
March	Other*	640	640
	Prunus spinosa	64	64
May	Other*	640	640
	Silene dioica	64	25
	Crataegus monogyna	64	64
July	Other*	640	640
	Centaurea nigra	64	25
	Rubus fruticosus	64	64

*Note that the 'other' category is a different set of pixels for each month

Table 2.4 Highest overall classification accuracies and kappa statistics achieved in each month for 3cm and 7cm resolution imagery

Classification	Overall Accuracy (%)		Kappa statistic	
	3cm	7cm	3cm	7cm
March	98.72	98.44	0.92	0.90
May	92.32	92.73	0.71	0.61
July	97.14	97.53	0.90	0.89

In March, the training set for the initial 3cm classification contained both pure and edge *Prunus spinosa* pixels. This resulted in an overall classification accuracy of 97.4%. The training set for a second 3cm classification variant contained only pure *P. spinosa* pixels, resulting in the classification with the best overall accuracy (Table 2.4). The difference between the two was only 1.3%.

The May classification iteration that resulted in the best overall accuracy also only used the pinkest *Silene dioica* pixels within the training set and excluded edge pixels. One iteration was very poor, classifying all pixels as *Crataegus monogyna*, resulting in a difference in overall accuracy of 84.0% between the most and least accurate classification iterations. The July classification iteration with the highest overall accuracy used the pure pixels for *Centaurea nigra* and *Rubus fruticosus* within the training set and not the edge pixels. Among the July classification iterations, the lowest overall accuracy was 60.0%, a difference of 37.1% from the highest (see Supplementary Data 1).

There was less than a 1% difference between overall accuracies for 3cm and 7cm classifications for each month respectively. March 3cm data resulted in higher overall accuracies than 7cm data, but the reverse was true for May and July data. The difference between kappa statistics for March, May and July were 2%, 10% and 1% respectively. The kappa statistic was higher for 3cm resolution imagery for each month.

2.3.2 User's and producer's accuracies

The user's and producer's accuracies for each flowering plant species in their respective 3cm and 7cm classifications can be seen in Table 3.5. These were calculated from the classification variants that gave the best overall accuracy (Table 2.4). It should be noted that these classifications did not necessarily have the best user's and producer's accuracies for individual species. For example, one 3cm classification iteration resulted in a user's accuracy of 100.0% for *Centaurea nigra* as opposed to the 91.8% shown in Table 2.5. On the other hand, the producer's accuracy for *C. nigra* in that 3cm classification iteration was only 26.6% (see Supplementary Data 1).

The difference between 3cm and 7cm classification user's accuracies for each species varied between 0.1% and 4.8%. User's accuracy was higher with 3cm imagery for all species other than *Rubus fruticosus* where it was higher with 7cm imagery. The difference between producer's accuracies for 3cm and 7cm imagery ranged between 3.1% and 12.1%. 3cm data resulted in higher producer's accuracies in all cases.

Table 2.5 Producer's and user's accuracies from the 3cm and 7cm classifications with best overall accuracy for each month

Classification Month	**Species**	**User's Accuracy (%)**		**Producer's Accuracy (%)**	
		3cm	**7cm**	**3cm**	**7cm**
March	*Prunus spinosa*	98.25	98.18	87.5	84.38
May	*Silene dioica*	95.35	92.86	64.06	52.00
May	*Crataegus monogyna*	77.78	76.09	65.63	54.69
July	*Centaurea nigra*	91.80	86.96	87.50	80.00
July	*Rubus fruticosus*	91.04	92.06	95.31	90.63

2.3.3 7cm training data

To verify whether 7cm data was a high enough resolution to train a classification, a training set was created for May using 7cm imagery which was then used to classify May 7cm imagery. The results of the accuracy assessment can be seen in Table 2.6 and the error matrix can be found in Supplementary Data 3 (accompanying the thesis digitally). The overall accuracy obtained for the 7cm classification when training the classifier with 7cm data was higher than both 3cm and 7cm classifications when trained with 3cm data. The user's accuracy for *Silene dioica* was lower, but producer's accuracy was higher, for the 7cm classification trained with 7cm data than for both 3cm and 7cm classifications trained with 3cm data. For *Crataegus monogyna*, user's accuracy for the 7cm classification trained with 7cm data was higher than both 3cm and 7cm classifications trained with 3cm data. *C. monogyna* producer's accuracy was higher for the 7cm classification trained with 7cm data than that trained with 3cm data, but the same as the 3cm classification trained with 3cm data.

Table 2.6 Overall, Producer's and User's accuracies for nectar-rich flowering plant species in May 7cm imagery when classified using the 7cm training set

Overall Accuracy (%)	Kappa statistic	User's Accuracy (%)		Producer's Accuracy (%)	
		Silene dioica	*Crataegus monogyna*	*Silene dioica*	*Crataegus monogyna*
94.65	0.73	85.71	85.71	72.00	65.63

2.4 Discussion

2.4.1 Suitability of 3cm and 7cm imagery for mapping nectar-rich flowering plant species

This study indicates that multispectral aerial imagery can be used to classify individual flowering plant species with high nectar-value to pollinators. For those classification variants that achieved the highest overall accuracies, these were well above the suggested target of 80-85% (e.g. see Foody, 2008 and Xavier et al. 2018). This is no surprise as the species under consideration had floral units with colours visibly distinct from the background vegetation (Dash et al., 2019). Kappa statistics were more variable, ranging between 0.61 for May 7cm imagery and 0.92 for March 3cm imagery. There is debate however, as to whether the kappa statistic is a useful metric for accuracy assessments in the first place (Bradter et al. 2020 and Foody, 2020).

It was clear that 3cm classification variants that excluded edge pixels within the training data for each month resulted in higher classification accuracies. This is likely because this reduces the spectral signature variability of pixels belonging to a particular flowering plant species category (Woodcock and Strahler, 1987). An alternative for dealing with mixed pixels in future studies could be to use a 'fuzzy' or 'soft' classification approach (e.g. see Foody & Arora, 1996; Shanmugam et al. 2006).

User's and producer's accuracies can be seen as more important for determining whether a particular flowering plant species has been correctly classified (Story & Congalton, 1986). For classifications with the best overall accuracy for each month and at each resolution, user's and producer's accuracies for *Prunus spinosa* and *Rubus fruticosus* were 80% or above. This is likely because although the floral units themselves are relatively small (Table 2.1), they flower in dense clusters within the hedgerow. Subsequently, there are likely to be fewer mixed pixels, which can reduce classification accuracies (Foody & Arora, 1996; Shanmugam et al., 2006). *Crataegus monogyna* also consisted of small floral units forming dense clusters. User's and producer's accuracies of less than 80% for *C. monogyna* within classifications trained with 3cm data were likely caused by spectral signature overlap with the synchronously flowering *Anthriscus sylvestris*, which can also flower in dense clusters (Figure 2.5).

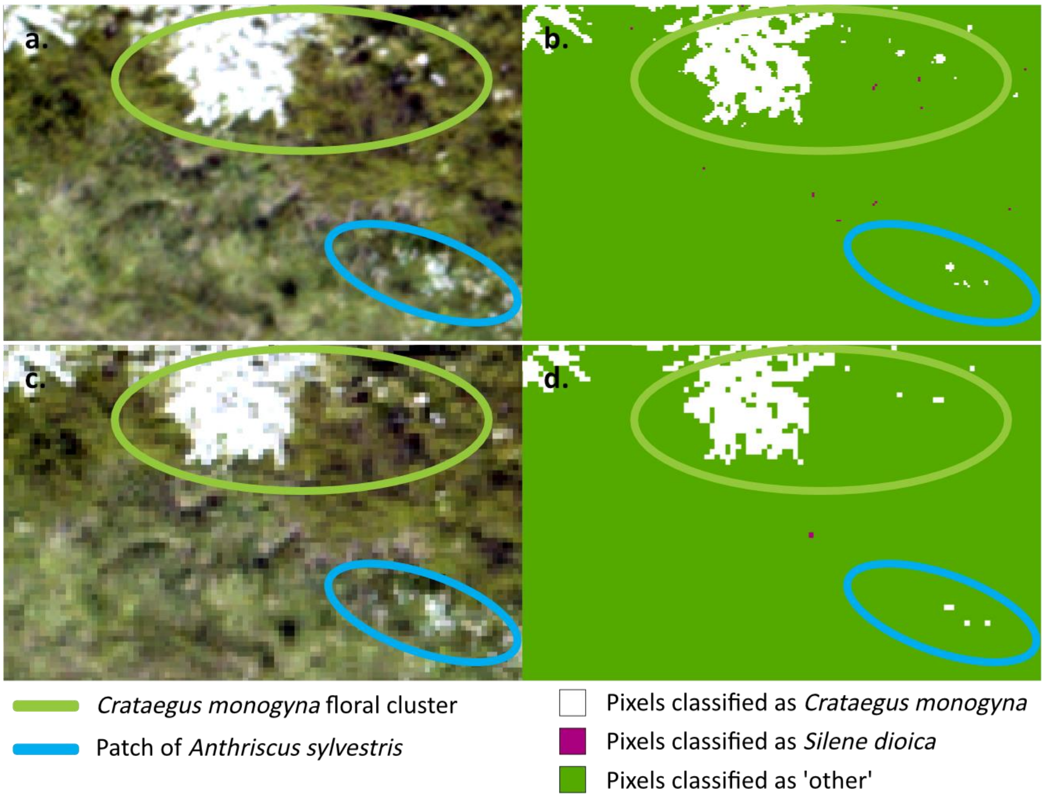


Figure 2.5 a. Subsection of the original May 3cm image with *Crataegus monogyna* and *Anthriscus sylvestris* circled **b.** The 3cm classification output with best overall accuracy showing pixels of *C. monogyna* correctly and incorrectly classified. **c.** Subsection of the original May 7cm image **d.** The 7cm classification output showing pixels of *C. monogyna* correctly and incorrectly classified.

User's and producer's accuracies obtained for *Centaurea nigra* in July were also 80% or above at each resolution. Despite similar floral unit sizes to *C. nigra* (Table 2.2), *Silene dioica* had producer's accuracies lower than 80% at each resolution, although the user's accuracies were higher. A possible explanation for differences between the two species is that the leafy vegetation in May was not as long as in July. It is therefore possible that other features with similar spectral characteristics to *S. dioica*, such as branches in the hedgerow, were more exposed in May than in July (Figure 2.6). Alternatively, many of the *S. dioica* floral units were positioned sideways rather than upright like the *C. nigra* units. This potentially meant that a smaller area of floral unit was seen from above, leading to pixels containing a greater proportion of other features. Although *S. dioica* floral units are bright pink, their sepals are dark purple, almost brown in colour. With the sideways positioning of *S. dioica* floral units and greater visibility of the sepals, it is possible that they were less spectrally distinguishable from other features such as branches when compared to *C. nigra's* bright purple, upwardly-oriented floral units.

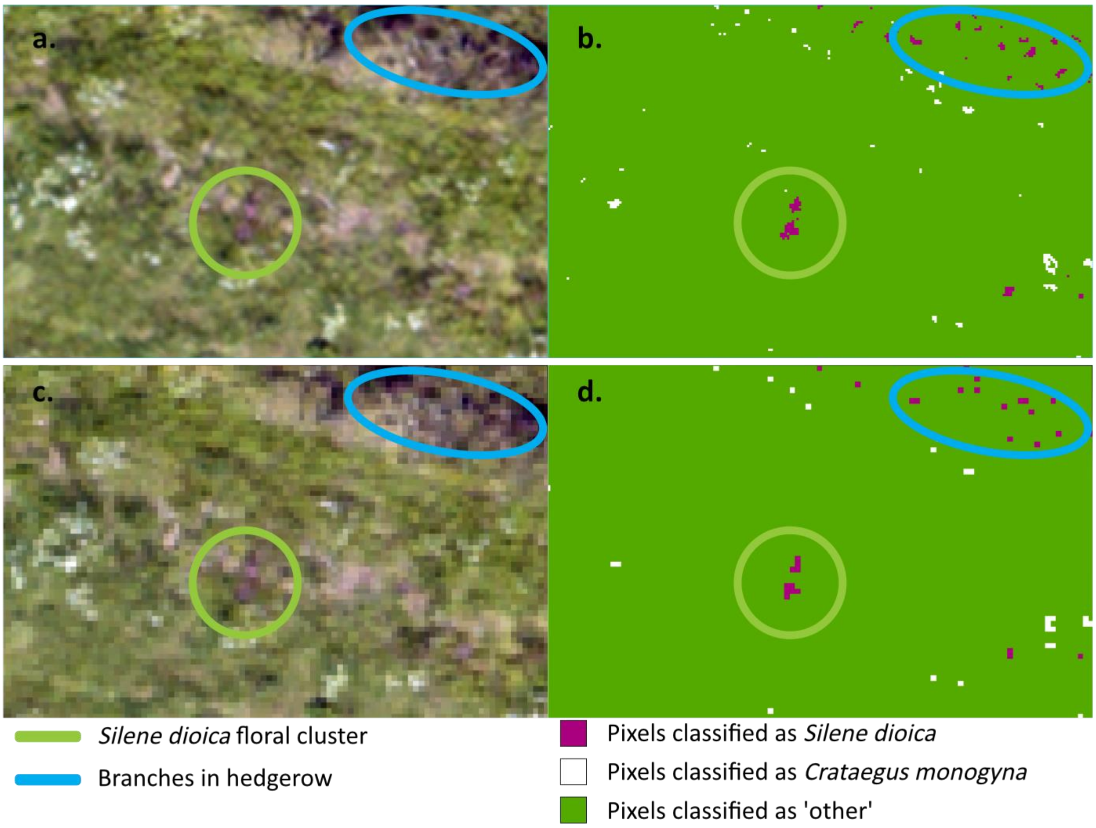


Figure 2.6 a. Subsection of the original May 3cm resolution image with *Silene dioica* and hedgerow branches circled. **b.** Subsection of the 3cm classification output with the best overall accuracy showing pixels of *S. dioica* correctly and incorrectly classified. **c.** Subsection of the original May 7cm image **d.** The 7cm classification output showing pixels of *S. dioica* correctly and incorrectly classified.

One way to address the misclassifications for both *C. monogyna* and *S. dioica* could be to combine spectral data with additional data such as vegetation height, for example through use of a decision tree (Sankey et al., 2018).

In each month the difference in overall accuracy between 3cm and 7cm imagery, when classified with 3cm training data, was less than 1%. In May and July, the 7cm classifications resulted in the higher accuracy. This suggests that the training data set prepared for the 3cm imagery was suitable for applying to the 7cm imagery. The 7cm classification for May trained with 7cm data resulted in an overall accuracy higher than both May classifications (3cm and 7cm) trained with 3cm data. In line with other studies (Latty et al., 1985; Toll, 1985), this suggests that higher spatial resolution is not always necessary to achieve good classification accuracies. This is not surprising because, spectral variability within classification categories can increase with a spatial resolution that is too high and which therefore picks up greater detail. There is subsequently a higher likelihood of different features having overlapping spectral signatures (Pu et al., 2011; Gong & Howarth, 1990; Latty et al., 1985; Toll, 1985).

2.4.2 Adapting the accuracy assessment process

In this study, verification pixels for use within the accuracy assessment process were selected in areas where we knew a particular species would not be growing. This is a similar approach to Holland and Aplin (2013), who only used accuracy assessment reference layer points that were linked to suitable ground-truth data. For example, it was assumed that pixels in areas of hedgerow not belonging to focal flowering plant species, such as patches of shadow, short grass paths, the crop edge, etc. would constitute ‘other’ category pixels. Pixels classified as *Centaurea nigra* in these areas were regarded as incorrect results.

These areas contained types of features that would likely be found in margin areas where *C. nigra* was flowering, e.g. leafy vegetation, dry vegetation, patches of soil. I therefore believe that this study is a good initial test of whether the selected species’ floral units can be detected using multispectral imagery.

However, I did not establish control sections in the long-grass margins where I knew focal species were absent. Other features in the margins that had not been accounted for could potentially also be classified as the flowering plant species of interest but would not be picked up within the accuracy assessment. Control areas containing species with potentially overlapping spectral signatures would be valuable in future studies, e.g. *Cirsium arvense* which in the study area was flowering synchronously to *C. nigra* albeit at a low abundance.

2.4.3 Mapping floral resources and the implications for pollinator management

Many studies have differentiated between broad floral/vegetation categories or gradients of floral composition with good degrees of success (e.g. see Xavier et al., 2018; Bradter et al., 2020, Feilhauer et al., 2013). Other studies have achieved high classification accuracies for individual plant species or species groups. When distinguishing between invasive *Pinus* species and native grassland vegetation for example, Dash et al. (2019) achieved kappa statistics higher than 0.996 when using cross-validation to verify different classification models.

In terms of flowers, Carl et al. (2017) used UAV imagery to estimate the number of *Robinia pseudoacacia L.* flowers per hectare in their study area: 5.3 million. Horton et al. (2017) successfully detected 84.3% of peach blossom pixels. With user's and producer's accuracies for *Rubus fruticosus*, *Centaurea nigra* and *Prunus spinosa* all above 80%, I achieved similar levels of accuracy for some species. To my knowledge, no others have attempted to use very high resolution remotely sensed imagery to map the floral cover of individual nectar-rich flowering plant species within arable field margins and hedgerows.

This is highly relevant for targeted pollinator management. Filling resource gaps at certain times of year could help avoid the disconnect between nectar supply and pollinator demand described by Timberlake et al. (2019). Timberlake et al. (2021) also demonstrate the importance of maintaining a continuous supply of nectar-rich flowering plant species across the pollinator foraging season. *Bombus terrestris* colony density was found to correlate with nectar provision in the late summer, highlighting the important role of flowering plant species such as *Hedera helix* at this time (Timberlake et al., 2021). Determining whether species that flower later in the year, such as *H. helix*, can be detected using the methods presented here would subsequently be hugely beneficial.

Furthermore, remotely sensed data could be used when planning where to locate new nectar and pollen resources, taking into consideration different pollinator foraging ranges (Greenleaf et al., 2007; Knight et al., 2005). Detailed knowledge of the spatiotemporal variation in habitat floral compositions could expand our understanding of pollinator-habitat relationships. Remotely sensed imagery has already been used to determine the links between habitat structure and avian species (Fritz et al., 2018).

High resolution floral data could be used to improve the predictive power of spatially-explicit models estimating pollinator abundance or pollination service provision across a farmed landscape (Lonsdorf et al., 2009; Gardner et al., 2020 and others). Tansey et al. (2009) suggest that fine scale remotely sensed data could be valuable to governmental bodies such as the UK Department for Environment, Food and Rural Affairs, in terms of measuring and monitoring biodiversity within farmed landscapes. The implementation of agri-environmental measures could be evaluated, in terms of their value to flower-visiting insects or their delivery of stated objectives related to floral resources (Tansey et al., 2009). This would be subject to the transferability of ground-truth data into an accurate map of resources for a wider range of nectar-rich flowering species, as discussed below.

2.4.4 Future research requirements

The potential for five key nectar-rich flowering plant species to be mapped at a single farm location with varying accuracies has been established through this study. Determining whether additional flowering plant species can be reliably and accurately mapped is an important area of future research. I found in this study that flowering plant species co-flowering with other species of a similar colour, had producer's and user's accuracies lower than species with no co-flowering similarly-coloured species. Although flower colour is an important determinant of the spectral signature of a flowering plant species, it is not the only determinant. Species could be spectrally separable from one another in the near-infrared region for example or, could have structural differences that influence their spectral signature. Building a database of those commonly found nectar-rich flowering plant species within a UK agricultural context that are or are not spectrally separable from co-flowering species within the same habitat type would be a useful next step. I start to address this in Chapter 4.

The prototype approach presented here can be extended to other species, taking into consideration the following suggestion. For 7cm imagery, I recommend that the number of floral units mapped on the ground be doubled to a minimum of approximately 200 floral units for species such as *Silene dioica* and *Centaurea nigra*, which have floral units of only several cm in width. This would provide a buffer should it not be possible to locate some of the floral units within the imagery, as was the case with the data in this study. As

I was unable to locate some of the floral unit clusters, I included 25 rather than the target 64 verification pixels for *S. dioica* and *C. nigra* in the May and July 7cm classification accuracy assessments respectively.

Scaling up the research to test the classification accuracy of nectar-rich flowering plant species at multiple locations across different agricultural landscapes could potentially form the basis of developing a spectral library of nectar-rich floral resources (Zhang et al., 2020). This could be used by land managers and other stakeholders to map resources for pollinators across farming systems. Constructing such a spectral library would be subject to converting digital number values to reflectance values and would require a detailed understanding of how the classification accuracy of floral resources is influenced by site conditions such as soil type (Pottier et al., 2014).

I have demonstrated through this study the accuracy with which known clusters of floral units for individual flowering plant species can be detected. I do not yet know the minimum cluster size that can be distinguished within the imagery and classified correctly, because I was not able to locate individual floral units. Quantifying this missing value is an important area for future work. It would also be important to quantify the mean number of flowers in a remote sensing unit as defined in the methods section. As was the case with *Silene dioica* in this study (see Figure 2.2 b, c), this can be different to the floral unit definition widely accepted within the pollinator research community and defined by Carvell et al. (2007). Once questions such as this are addressed, for those species with high enough user's/producer's accuracies, we would potentially be able to estimate nectar provision at a farm scale, e.g. using values from Baude et al. (2015a). A simpler option may be to determine whether the area classified as a particular flowering plant species is correlated with the number of floral units of that species on the ground. This is an approach that I use in the following Chapter.

If certain flowering plant species remain spectrally inseparable at the species level, they may still be separable into functional groups. Groups would have to be constructed based both on their properties that make them spectrally distinguishable from another group, as well as those that make them attractive/accessible to pollinators, e.g. nectar sugar content (Kattenborn et al., 2019; Fornoff et al., 2017; van Rijn and Wäckers, 2016).

Classifying flowering plant species in combined classification categories is an area that I explore in Chapter 4.

Alternatively, for those species not separable with multispectral imagery, it could be worthwhile investigating the use of hyperspectral imagery (e.g. see Underwood et al., 2007; Kattenborn et al., 2019). Feilhauer et al. (2016) did not look at individual species, but demonstrated that plant pollination types (wind, insect or self-pollinating) could be distinguished and mapped using hyperspectral remote sensing. This was linked to the fact that they vary as to their canopy structure and leaf traits. For example, plants typically pollinated by insects tended to have a greater leaf area index when compared to wind-pollinated species (Feilhauer et al., 2016). Using hyperspectral data does not always guarantee higher accuracies than the levels achieved through this study. When producing maps of white flowering and yellow flowering trees in Kenya, among other land use/land cover (LULC) classification categories, Abdel-Rahman et al. (2015) obtained overall accuracies of 88.2% and 83.7% when using hyperspectral data for February 2013 and January 2014 respectively. On the other hand, user’s and producer’s accuracies were below the 80-85% accuracy threshold (Xavier et al. 2018, and Foody, 2008) for some of their LULC categories (Abdel-Rahman et al., 2015). With the higher costs involved with hyperspectral data, it would subsequently be important to determine whether the additional cost is worth any increases in accuracy metrics obtained (Galbraith et al., 2015).

As noted in the introduction, I chose to use a maximum likelihood (ML) classifier due to its ready availability (Lu and Weng, 2007) and its ease of use for applications on the ground, i.e. it is available through platforms such as the QGIS Semi-automatic Classification Plugin (SCP) (Congedo, 2016; QGIS 2020). Nonetheless, with future studies it would be interesting to compare the performance of an ML classifier to a machine-learning approach. This would be particularly valuable as freely available software with easy-to-use graphical user interfaces, such as the SCP QGIS plugin, have started to develop machine-learning tools since the completion of this study (Congedo, 2021). Machine-learning approaches are non-parametric and therefore do not rely on normal distributions within data (Belgiu and Drăguţ, 2016; Lu and Weng, 2007), nor do they require any prior understanding of how data relate to one another (Lary et al., 2016).

They are also better able to deal with heterogeneity within classification categories (Grinand et al., 2013).

2.5 Conclusion

I demonstrate that five nectar-rich pollinator foraging resources can be mapped using multispectral data with very high spatial resolutions of 3-7cm. Regardless of month of data acquisition and spatial resolution, overall accuracies are all high, ranging from 92.3%-98.7%. Producer's and user's accuracies for individual species are more variable. High classification accuracies are achieved for some species such as *Prunus spinosa* (98.3% user's accuracy and 87.5% producer's accuracy for 3cm classifications). Lower accuracies are associated with species flowering concurrently to other flowering species with similar spectral properties or, at times of year when non-vegetation features with similar spectral properties such as branches are more exposed. Questions remain in terms of improving these lower user's and producer's accuracies. Nonetheless, a foundation has been provided upon which to build this work. Remotely sensing floral and other habitat resources will be increasingly valuable into the future as one of many management tools that can help prevent further pollinator declines.

Chapter 3

Modelling the margin-level bee abundance as a function of the total nectar sugar supply and nectar sugar proxies

3.1 Introduction

As I review in Chapter 1, intensively farmed arable landscapes often have a limited supply of floral resources available to pollinators (Baude et al., 2016; Goulson et al., 2015; Potts et al., 2016; Timberlake et al., 2019; Jachuła et al., 2021). This is due to a combination of habitat reduction (Goulson et al., 2015) and degradation as a result of intensive agricultural management, for example through the use of herbicides which can reduce the availability of foraging resources (Gabriel and Tscharntke, 2007; Potts et al., 2016). However, much global research has investigated how farm management and increasing flower-rich habitats and overall floral availability in agricultural landscapes can increase pollinator metrics such as abundance and richness (Holland et al., 2017; Lowe et al., 2021; Scheper et al., 2013).

Rather than considering total floral abundance or floral cover, studies are increasingly focusing upon nectar sugar availability at the national (Baude et al., 2016), regional (Jachuła et al., 2021) or farm scale (Timberlake et al., 2021), as a result of its importance to pollinators as a prime energy supply (Brodschneider and Crailsheim, 2010; Nicolson et al., 2011; Willmer, 2011). These studies primarily focus upon the nectar-provision of broad habitat categories, rather than considering the fine-scale within-habitat nectar variability (although see Hicks et al., 2016). Subsequently, although the diversity (Mallinger et al., 2016), proportion (Lowe et al., 2021; Scheper et al., 2013) and spatial structure of habitat (Martin et al., 2019) all shape local pollinator communities, there is great scope to investigate how the within-habitat nectar supply influences pollinator abundance at the local scale. This Chapter therefore focuses on the relationship between the nectar supply in arable field margins and margin-level bee abundance.

3.1.1 Nectar-availability as the key pollinator energy source

As considered in Chapter 1 (Section 1.3), simply increasing floral abundance or diversity in an arable landscape does not by default mean that all of the nutritional requirements needed to conserve and maintain healthy pollinator communities are being met (e.g. Vaudo et al., 2015; Willcox et al., 2018). Timberlake et al. (2021) for example, found that there was no significant relationship between nectar provision and the proportion of flower-rich habitat. Additionally, while bumblebee colony density could be predicted by nectar production in the autumn, it could not be predicted by floral abundance (Timberlake et al., 2021). The authors subsequently urge caution if using flower-rich habitat or floral abundance as a proxy for pollinator foraging resources (Timberlake et al., 2021).

An alternative therefore, is to focus on the fine-scale distribution of individual floral resources, such as pollen and nectar. Correlations between nectar supply and pollinator richness and abundance have already been demonstrated. Holl et al. (1995) in Virginia, USA for example, found a strong positive relationship between the quantity of nectar sugar produced (g) and, species richness and abundance of butterflies across reclaimed sites that were previously surface-mined for coal.

Nectar supply can vary considerably according to season and habitat-type (Baude et al., 2016; Timberlake et al., 2021). Across Great Britain for example, the greatest proportion of nectar (60%) is produced in July/August (Baude et al., 2016). Nectar sugar supply from different habitats also varies considerably, with arable land producing 6.9 kg/ha/year, compared to calcareous grassland which produces 97.5 kg/ha/year. In a Belgian study, Langlois et al. (2020) found that overall, extensively farmed landscapes produced a greater quantity of nectar than intensively farmed landscapes (105 g/ha/day for the former as opposed to 58 g/ha/day for the latter), although differences between the two varied according to time of year. There was no difference in nectar production between both landscape types in May for example, as a result of the mass flowering of *Brassica napus*. However, extensively farmed landscapes produced more than four times the quantity of nectar sugar in June when compared to intensively farmed landscapes.

Understanding the spatial and temporal variation in nectar supply is essential if we are to better target on-farm conservation interventions to meet the resource requirements of a pollinator community. Until we know where the nectar-resource gaps are, we cannot address them. For example, Timberlake et al. (2019) found that variation in nectar demand from *Bombus* species, did not perfectly match spikes and dips in nectar supply throughout the foraging season. Nectar supply was particularly low in the early spring, June and mid-summer. This could be problematic for species with high energy demands at those times (Timberlake et al., 2019).

Jachuła et al. (2021) similarly found that the nectar supply in Polish upland landscapes did not meet honeybee (*Apis mellifera*) nectar demand in March and June or bumblebee (*Bombus* sp.) nectar demand in June. This corroborates the findings of Timberlake et al. (2019) and highlights that very different European agricultural regions experience nectar gaps at these times. However, it should be noted that both studies only estimate the nectar demand of a limited range of taxa. Should the nectar demand of other pollinator species also be calculated, it is possible that discrepancies in supply and demand could arise at different times of year due to varying pollinator phenology (Hennessy et al., 2021; Ogilvie and Forrest, 2017) or, the already-identified gaps between nectar supply and demand for honeybees and bumblebees could be enhanced further.

In addition, the nectar supply at a given point in time not only provides an energy source for pollinators active at the time (Willmer et al., 2011) but, can also influence the survivability and reproductive success of pollinator communities. This is demonstrated by Timberlake et al. (2021), who found a significant positive relationship between nectar supply (g/km^2/day) in the late summer and *Bombus terrestris* colony density (colonies / km^2) the following summer.

3.1.2 Fine-scale nectar sugar variation between field margins

Various studies (e.g. Baude et al., 2016; Jachuła et al., 2021; Timberlake et al., 2019) have estimated nectar sugar production according to broad habitat categories such as ‘field margins’, ‘hedgerow’, ‘improved grassland’, ‘broadleaf woodland’, ‘road verges’ and so on. Many of these studies will miss the fine-scale within-habitat variability in the nectar resource. Jachuła et al. (2021) did account for some within-habitat variability in nectar-rich flowering plant species, by measuring the nectar production values of a wide range of created habitat types (e.g. road verges, field margins and fallow land), including in sub-habitat categories. For example, field margins were grouped according to the size of the fields that they bordered. However, this does not account for other factors that may influence variability in margin-level plant species composition, flower density or diversity, such as choice of sown seed mix and the success of their establishment (Cresswell et al., 2019), the local seed bank (Robinson and Sutherland, 2002) and field margin management (Pywell et al., 2011).

Baude et al. (2016) calculated the national nectar provision of particular UK-based agri-environment Environmental Stewardship options (e.g. the EF4/HF4 'nectar flower mix' and HE10 'Floristically-enhanced grass buffer strip'). However, the recommendations for managing EF4/HF4 and other agri-environment interventions are broad and, include an element of species selection (Defra, 2013). This means that flowering plant species compositions and the subsequent nectar provision could still vary substantially, even within the same margin intervention type. Hicks et al. (2016) did not relate their data to pollinator abundance but, did compare the nectar sugar production of annual mixes (10.8 $mg/m^2/day$ and 10.6 $mg/m^2/day$ for each annual mix respectively) to that of a perennial mix (67.5 $mg/m^2/day$), the latter producing a significantly greater nectar quantity ($p < 0.05$).

I am not aware of any studies looking at how nectar rather than floral abundance or cover vary within broad agricultural semi-natural habitat types and then relating this to pollinator abundance. Timberlake et al. (2021) modelled the impact of sowing all field margins at their study farms with an Environmental Stewardship 'EF4' mix relative to the baseline (which varied according to farm). This would increase the nectar productivity of field margins and subsequently, the model predicted that *Bombus terrestris* colony density would increase by 207% (Timberlake et al., 2021).

There is great potential for exploring the variability in nectar resources in the same agricultural habitat types further and, the relationship with pollinator abundance as I do in this Chapter. I focus on calculating the relationship between the fine-scale variability in the nectar sugar supply and bee abundance in arable field margins in an intensively farmed agricultural system. I chose this habitat type because they are often employed as a means of providing pollinator resources in agricultural landscapes, yet the resources that they provide vary considerably (Cole et al. 2020).

3.1.3 Floral abundance as a proxy for nectar availability

As reviewed in Chapter 1 Section 1.8 and Chapter 2, remotely-sensed imagery with spatial resolutions of several centimetres has been used to map the floral component of various species (Carl et al., 2017; Horton et al., 2017). There is huge potential to apply remote-sensing technology to the mapping of pollinator foraging resources (Szigeti et al., 2016; Xavier et al., 2018). This was the focus of Chapter 2, in which I used very high resolution multispectral imagery to classify five nectar-rich flowering plant species that constitute important pollinator foraging resources. Imagery was acquired via a manned aircraft and had spatial resolutions of 3cm and 7cm, respectively. Classification accuracies ranged from 92.3% to 98.7% for overall accuracy and between 52.0-95.3% and 76.1-98.3% for producer's and user's accuracies, respectively. I continue this process in Chapter 4, using imagery acquired via an unmanned aerial vehical and expanding upon the questions addressed in Chapter 2.

However, while remote sensing can save time at the fieldwork stage, processing and classifying imagery can be time-consuming. Rather than mapping and classifying all potential entomophilous species that may be encountered in an arable landscape, it would therefore be useful to concentrate efforts on mapping only a sub-set of the foraging species. I ask as a second aim in this study, whether the nectar sugar supply of a subset of the flowering plant species present at a study farm based in the UK can be used as a proxy for the total nectar sugar supply (mg/m^2/day) when predicting bee abundance.

3.1.4 Research questions

Various studies have focused on the relationship between the nectar sugar supply and pollinator abundance (Holl et al., 1995; Jachuła et al., 2021; Timberlake et al., 2021). To complete a remaining research gap, I focus on two different margin types commonly found in agricultural landscapes, the first type being margins allowed to regenerate naturally and the second being margins sown with a commercial grass and wildflower mix. The two margin types are likely to provide a range of nectar sugar values, as naturally regenerated margins and those sown with a wildflower mix have different plant compositions (Pywell et al., 2005). I hypothesize that:

2.) As the mean total nectar sugar provision (mg/m^2/day) of arable field margins increases, the margin-level bee abundance also increases.

Section 3.1.3 noted the value of focusing remote sensing efforts on those flowering plant species that contribute the most pollinator foraging resources i.e., of relevance to this study, the highest nectar producers. The total nectar supply at the margin level is a function of both floral abundance and the nectar productivity of individual flowering plant species (Baude et al., 2016). I therefore propose in this study, to determine whether the flowering plant species that produce the greatest proportion of the nectar resource across the arable field margins of each type (naturally regenerated and sown), can be used as a proxy for the total nectar sugar supply. Specifically I hypothesize that:

3.) The combined margin-level nectar sugar provision (mg/m^2/day) of the flowering plant species that contribute the greatest proportion of the nectar sugar within each margin type respectively, is positively correlated with bee abundance.

3.2 Materials and Methods

3.2.1 Study sites

The study sites were located on a conventional arable farm in Northamptonshire, UK. For a complete description of the study farm, see Chapter 2 (Section 2.2.1). The farm had two main sites (approximately 7.98km apart; co-ordinates for approximate centre of site 1 = 52°18'9"N, 0°45'41"W and co-ordinates for approximate centre of site 2 = 52° 13' 51"N, 0° 46' 18"W). 16 field margin sections were included. Eight margins were sown with the KWM2bs wildflower mix produced by Kings Crops (Frontier Agriculture Ltd., 2021), hereafter referred to as “Kings”. The full list of wildflower species included in the Kings mix can be found in Appendix 3.1. Kings mixes were mown once a year in the late summer following completion of harvest. The remaining eight margins had been allowed to regenerate naturally, hereafter referred to as “NatReg”. Management of NatReg margins was minimal, consisting of cutting back the vegetation to the ground every few years. The NatReg margin sections consisted primarily of stands of *Rubus fruticosus*, *Urtica dioica* or grass, interspersed with other species such as *Heracleum sphondylium* or *Cirsium arvense*.

All Kings margin sections were 6m wide and ran parallel to the cropped area immediately adjacent to the crop. Three NatReg margins were 6m wide and ran parallel to the cropped area with a grass path between the crop and margin to allow vehicles to pass. The remaining five NatReg "margins" were actually patches of naturally regenerated habitat rather than margins, being wider than 6m and not necessarily forming a rectangular margin shape. In these instances, 6m wide sections in the NatReg patches were surveyed for consistency. Maps outlining the location of each margin or patch relative to the cropped area can be seen in Figure 3.1.

Margin sections were at least 500m apart to reduce the probability of surveying individual bees from the same community (Greenleaf et al., 2007). Distances of ≥500m between margin sections were verified by creating a 500m wide buffer around polygons outlining each margin section in QGIS version 3.4 (QGIS, 2020) and checking that no margin buffers were overlapping another margin section polygon.

3.2.2 Semi-natural habitat area

While the primary aim of this study was to focus on field margins as a habitat type, the proportion of semi-natural habitat in a landscape can also influence bee abundance (Lowe et al., 2021; Scheper et al., 2013). The proportions of semi-natural habitat immediately surrounding each margin were therefore calculated within 250m radii.

The UK Centre for Ecology and Hydrology (UKCEH) produce yearly land cover maps for the entirety of Great Britain using satellite imagery (UKCEH, 2021). The Land Cover Map layer for 2019 (LCM2019), a raster layer with 25 X 25m pixels (Morton et al., 2020), was downloaded into QGIS. The raster was converted into a vector layer. Buffers with a 250m radius were created around each margin section polygon. The QGIS 'intersection' tool was then used to intersect the vectorised LCM2019 layer using the buffers. The proportion of semi-natural habitat surrounding each margin section was subsequently calculated.

A 250m radius was selected as this meant that radii around each margin were not overlapping and proportions of semi-natural habitat at this level were independent. However, bee foraging ranges can be higher than 250m (Greenleaf et al., 2007) and so the proportions of semi-natural habitat within 500m radii were also calculated as a separate analysis to see whether the results at this wider level remained consistent.

Semi-natural habitat in the study farm landscape included both 'Deciduous woodland' and 'Neutral grassland' UKCEH Land Cover categories (UKCEH, 2020). It should be noted that the UKCEH LCM2019 does not include field margins or hedgerow. I acknowledge that this may mean that the true proportion of semi-natural habitat surrounding each margin section is underrepresented. However, the majority of fields on the farm are surrounded by 6m wide margins as a minimum and hedgerow. It is unlikely therefore, that the proportions of hedgerow and field margin habitats vary considerably within the buffers surrounding each margin section.

3.2.3 Floral surveys

Floral resources were surveyed in each of the 16 margins in 2019 between 20th June and 23rd July. Linear transects were marked out 3m into the margin from the margin edge. Ten 1m^2 quadrats were placed every 10m along a 100m transect, with the first quadrat placed 10m along the transect to avoid field corners. The side of the transect on which the quadrat was placed (left or right), and the distance from the transect line (0, 1 or 2m) were both randomly selected using the Excel 'RandBetween' function (Microsoft, 2021a). Figure 3.2 outlines the set-up for the quadrat surveys.

a.)


Margin 7
Margin 6
Margin 9
Margin 8
Margin 1
Centre of site 1
Margin 5
Margin 2
Margin 4
Area 1
Margin 3
Google Earth
N
1 km

b.)

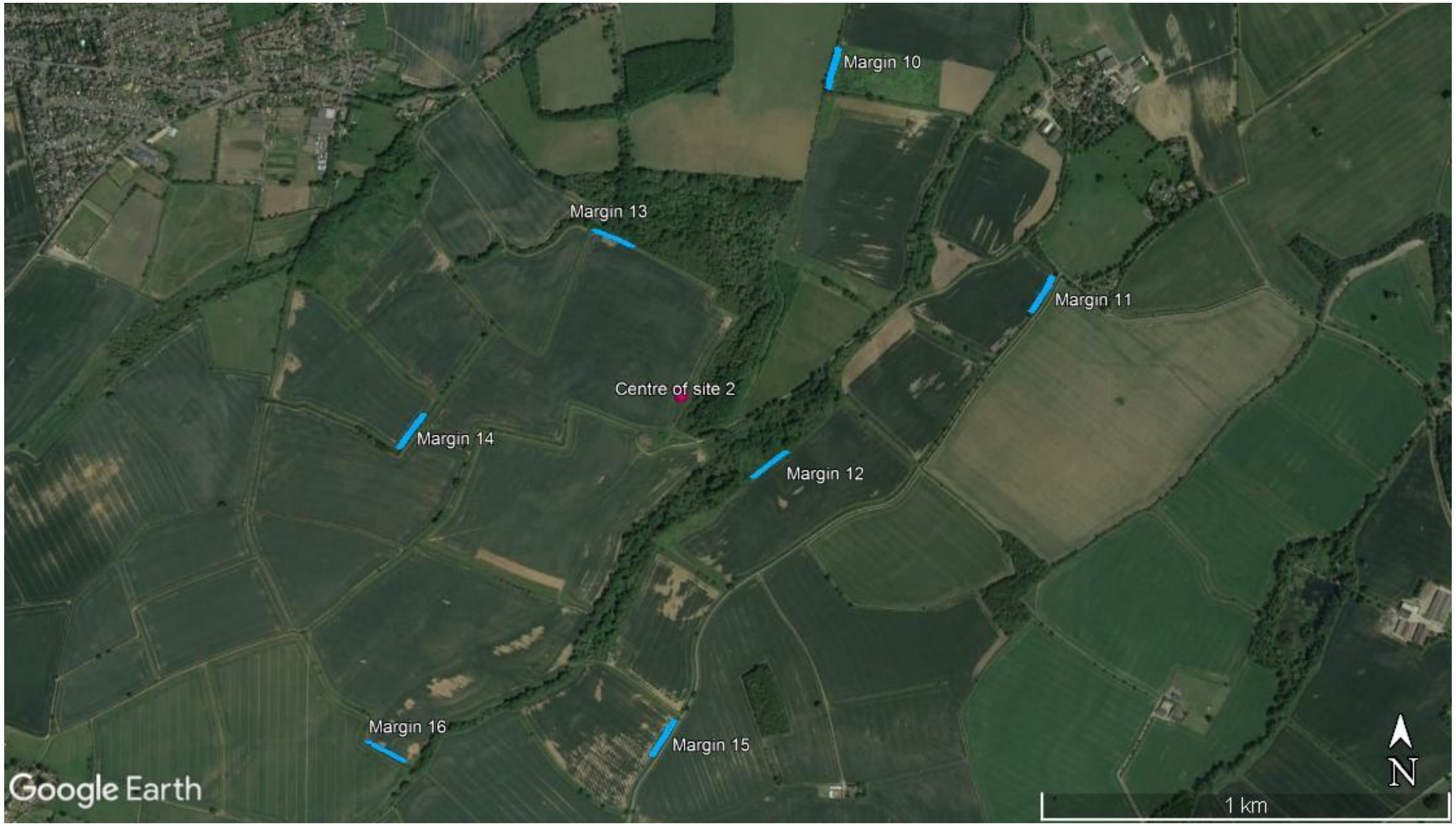


Figure 3.1 (a) Farm site 1 with margins 1 – 9 in blue (Google Earth Pro V 7.3.4.8642, 2020b). The approximate centre site centre is marked by a purple point (coordinates 52°18'9"N, 0°45'41"W). **(b)** Farm site 2 with margins 10 – 16 marked in blue (Google Earth Pro V 7.3.4.8642, 2020c). The approximate site centre is marked by a purple point (52° 13' 51"N, 0° 46' 18"W) and is ~7.98km away from the centre of site 1. See Figure 1.4 in Chapter 1 for the location of these sites in the context of each other.

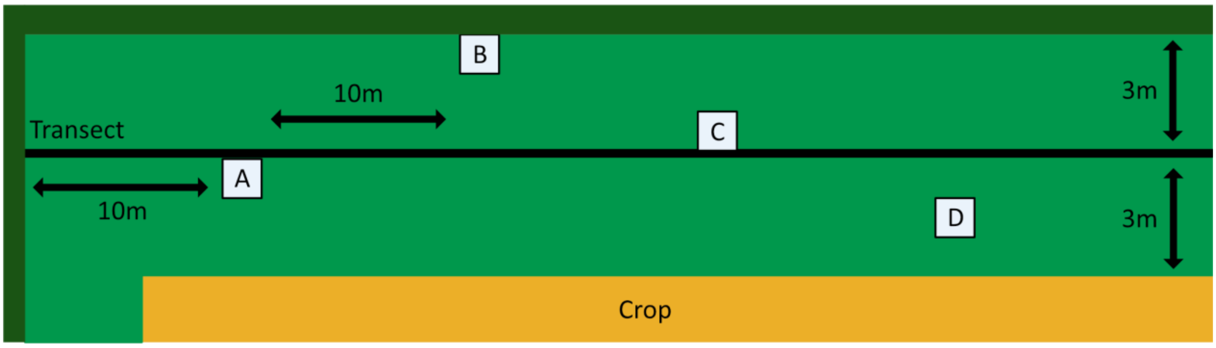


Figure 3.2 Set-up for quadrat surveys. Quadrat A is located 10m along the transect from the edge of the field. The remaining quadrats are spaced 10m apart along the transect. The positioning of each quadrat is randomly selected. The random positioning for quadrat B for example, was 2m to the left of the transect. Only the first 50 m of the transect, and four of 10 quadrats are shown.

The floral units of all entomophilous plant species with open flowers at the time of surveying were counted in each quadrat. Floral units were defined as either individual flowers or stems with multiple flowers that a bee can walk rather than fly between, e.g. one *Centaurea nigra* capitulum (Carvell et al., 2007). Flowering plant species were identified and named according to Stace (2010).

3.2.4 Bee surveys

Bee surveys were carried out between June 20th and July 23rd 2019, in the same margin locations. Three bee surveys were carried out for each of the 16 margin sections. Each of the three surveys were carried out on a different date and at a different time of day: one in the morning (09:00-12:00hrs), one at 'midday' (12:00-14:00hrs) and one in the afternoon (14:00-17:00). All bee surveys were carried out within two weeks of the floral resource surveys, either before or after. Surveys were carried out in conditions that met Butterfly Monitoring Scheme criteria: 17°C with 60% sunshine or 13°C with complete sunshine and, no more than Beaufort Scale 5 winds (Pollard and Yates, 1993). Wind speed was measured using an anemometer at the start of each bee survey. The air temperature (°C) in the shade was measured at the start of each survey using a digital thermometer (see Supplementary Data 4, digitally accompanying the thesis). However in two instances this was not possible (survey 1 of margin 2 and survey 1 of margin 3). In these two instances, temperature was recorded from the Pitsford local weather station (~9.8km from margin 2 and ~10.0km from margin 3, which has information updated online and via an app every 10 minutes (Pitsford School, 2021).

Surveys were carried out along a 120m transect that was walked at a steady pace. The survey start and end times were recorded and the time taken to survey can be found in Supplementary Data 4. The transect zig-zagged across the 6m-wide survey area (see Figure 3.3). The direction in which each margin transect was walked was randomly selected in Excel.

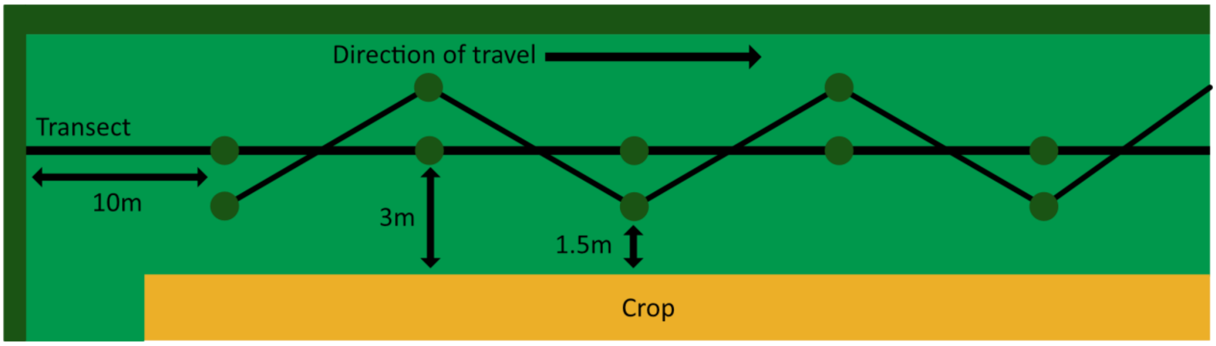


Figure 3.3 Transect set-up for bee surveys showing the 'zig-zag' pattern that was walked.

All bee species seen visiting floral units within 1m on either side of the surveyor and the flowering plant species on which they were foraging was recorded. No distinction was made as to whether bees were foraging for pollen or nectar. Bees were identified as being either *Bombus* (bumblebees), *Apis mellifera* (honeybees) or any other species (hereafter termed solitary bees).

3.2.5 Statistical Analysis

3.2.5.1 Bee abundance models

I first addressed the hypothesis that bee abundance is positively correlated with the nectar sugar supply across margins. Honeybee abundance data and wild bee abundance data were aggregated across the three surveys for each margin, to obtain the total honeybee abundance and total wild bee abundance respectively, for each of the 16 margins. Analysis of covariance (Ancova) generalised linear models (GLMs) were carried out in R version 4.0.5 (R, 2021) following Crawley (2005). I first modelled total honeybee abundance as a response variable, hereafter called Bee_{Hon}. I next modelled total wild bee abundance as the response variable, hereafter Bee_{Wild}. This included bumblebees and solitary bees only. I modelled honeybee abundance and wild bee abundance separately, as the former could mask the relationship between nectar supply and wild bee abundance due to honeybee recruitment strategies (e.g. Seeley et al., 1991).

Continuous explanatory variables included in the original models for Bee_{Hon} and Bee_{Wild} were total mean nectar sugar (mg/m^2/day) for each margin and mean air temperature (°C) during bee surveys (mean temperature across the three surveys for each margin). Mean nectar sugar (mg/m^2/day) for each margin was obtained by multiplying the mean floral unit count (floral units / m^2) for each flowering plant species, with the mean quantity of nectar sugar produced by a floral unit of that species (mg / floral unit / day). The mean nectar sugar produced per floral unit was obtained by multiplying the mean nectar sugar per flower (Baude et al., 2015a) by the mean number of flowers per floral unit (Baude et al., 2015b). However, the mean nectar sugar per flower was not available for *Vicia hirsuta* in the Baude et al. (2015a) dataset and so the nectar sugar values from Hicks et al. (2016) were used. No nectar sugar value was available for *Onobrychis viciifolia* or any species within the *Onobrychis* genus. This species was therefore left out of the models, but it is unlikely to have contributed to the nectar sugar supply to any great extent as only five *O. viciifolia* floral units were counted across 160 1m^2 quadrats. One species was unidentified and left out of the models, but only one floral unit of this species was found across 160 quadrats and again was unlikely to be contributing to any great extent to the nectar sugar supply.

Margin type (Kings or NatReg) was included as a categorical explanatory variable in the Bee_{Hon} and Bee_{Wild} models. A Mann-Whitney U test was used to determine whether there was a significant difference between the mean nectar sugar (mg/m^2/day) produced by each margin type (Kings and NatReg).

As the bee abundance data were count data, a Poisson error distribution was initially used in the Bee_{Hon} and Bee_{Wild} models (Crawley, 2005). As the initial models were overdispersed, the models were re-run using quasipoisson (Crawley, 2005). The Bee_{Hon} and Bee_{Wild} models were then simplified and each new model was compared with the previous one using Anova, to make sure that there was no significant loss of explanatory power (Crawley, 2005). Any non-significant variables and their interactions were removed one by one, starting with the highest order variables first (See Tables 3.1 and 3.2 in the results Section 3.3.1 for the order in which variables were removed). The data from the Bee_{Hon} and Bee_{Wild} models with the best fit were then plotted using ggplot2 (Wickham et al., 2016). Estimates of pseudo-R^2 were calculated for the Bee_{Hon} and Bee_{Wild} models (R^2 cannot be calculated for Poisson/quasipoisson models (Smith and Warren, 2019)). Each model was checked for normally distributed errors using a Normal Q-Q plot and constancy of variance using a residuals vs fitted values plot. Cook's distance plots were used to check for influential points.

3.2.5.2 Sensitivity analyses

For both the Bee_{Hon} and Bee_{Wild} models, a number of sensitivity analyses were carried out, all of which can be found in Appendix 3.2 and none of which affected the relationship between the explanatory variables and bee abundance at the margin level. If there had been uncertainty surrounding the identification of a species such as *Epilobium tetragonum*, the Bee_{Hon} and Bee_{Wild} models were re-run while first doubling and then halving the nectar values for those species. If nectar-values were only available for one member of a genus, as was the case with *Myosotis,* where the only species nectar value available was for *Myosotis arvensis*, all species in that genus were given the available nectar value in the Bee_{Hon} and Bee_{Wild} models. However, in the sensitivity analyses the models were again re-run while halving and doubling the nectar values for the other species within the genus for which individual nectar sugar values were not available.

If nectar sugar values were available for two or more members of a genus but not the species under consideration, as was the case with *Lathyrus nissolia*, the most conservative nectar sugar value for the genus (the value for *Lathyrus pratensis* in this example) was allocated to the species in the Bee_{Hon} and Bee_{Wild} models. In the sensitivity analyses, the models were re-run several times. First the least conservative nectar sugar value for the genus (the value for *Lathyrus latifolia* in this example) was used and then, the most and least conservative nectar sugar values for the genus were doubled and halved respectively.

For four flowering plant species (*Prunella vulgaris*, *Lotus corniculatus*, *Galium album* and *Vicia hirsuta*), my interpretation of one floral unit was different to the interpretation of Baude et al. (2015b). I counted one stem of *P. vulgaris* as a floral unit for example, as the flowers were in close proximity to one another, i.e. a bee could walk rather than fly between flowers (Carvell et al., 2004). Baude et al. (2015b) counted each individual *P. vulgaris* flower as a floral unit. In the Bee_{Hon} and Bee_{Wild} models, nectar supply was estimated at the margin level using the floral unit definitions of Baude et al. (2015b), i.e. abundance counts were included in the model as single flowers when they were really counts of inflorescences, as I had not counted the number of individual flowers per floral unit. In the sensitivity analyses, data from a separate survey (at the same study farm) was used to estimate the maximum number of flowers encountered in my definition of a floral unit for *P. vulgaris*, *L. corniculatus and Vicia hirsuta.* The Bee_{Hon} and Bee_{Wild} models were then re-run using the maximum potential number of flowers (maximum encountered through my separate survey at the study farm) found in a single unit of *P. vulgaris*, *L. corniculatus* and *Vicia hirsuta* and their associated nectar values. Data for the maximum potential number of flowers in a *G. album* unit was not available but, this is unlikely to have made a difference to the overall nectar sugar supply due to the very low nectar sugar production of *G. album* (0.004 mg/flower/day).

3.2.5.3 Total nectar sugar supply proxy

A cumulative frequency curve was produced to demonstrate the contribution of each individual entomophilous plant species to the total nectar sugar supply across the 16 margins. The contribution of each entomophilous plant species to the nectar sugar supply of each type of margin (Kings and NatReg) respectively, was also calculated. The lists of species for each margin type respectively were ranked according to their nectar sugar production values (mg/m^2/day).

I tested whether the nectar sugar supply of the entomophilous plant species contributing the greatest proportion of the nectar sugar supply in each margin type (NatReg and Kings) could be used as a proxy for the total nectar sugar supply. The Bee_{Hon} and Bee_{Wild} models were run a second time but, the total margin-level nectar sugar supply was replaced with the margin-level nectar sugar supply (mg/m^2/day) of the species contributing a minimum of 75% of the nectar sugar supply in each margin respectively. These were *Centaurea nigra* for the Kings margins (contributing 90.6% of the nectar sugar supply) and *Rubus fruticosus*, *Cirsium arvense* and *Chamerion angustifolium* for the NatReg margins (together contributing 81.4% of the nectar sugar supply in NatReg margins). These models are hereafter called Bee_{Hon_Prop} and Bee_{Wild_Prop} and, model honeybee abundance and wild bee abundance respectively. Margin type and mean temperature were again included as explanatory variables. A quasipoisson distribution was used for the Bee_{Hon_Prop} and Bee_{Wild_Prop} models and each model was simplified following the same method as for the Bee_{Hon} and Bee_{Wild} models (see Section 3.2.5.1). Estimates of pseudo-R^2 were calculated (Smith and Warren, 2019). Models were again checked for normally distributed errors, constancy of variance and influential points.

3.2.5.4 Semi-natural habitat

A Mann-Whitney U test was carried out to determine whether there was a difference between margin types (NatReg and Kings) in terms of the proportion of semi-natural habitat present within each 250m radius. The analysis was repeated separately for the 500m radii.

3.2.5.5 Floral species richness

The main aim of this study was to focus upon the margin-level nectar sugar availability (mg/m^2/day) and its relationship with bee abundance. However, floral species richness can sometimes influence bee abundance (Scheper et al., 2013). I therefore used a Spearman's Rank Correlation Test to determine whether there was a correlation between the margin-level species-richness and bee abundance. A Mann-Whitney U test was used to test for any differences in species richness between Kings and NatReg margins.

3.3 Results

A total of 11436 floral units were counted across 16 margins (eight NatReg and eight Kings). A total of 6010 floral units were counted across NatReg margins and, a mean of 69.2 ± 24.6 floral units / m^2 (1 S.E., n = 8). A total of 5426 floral units were counted across Kings margins and, a mean of 67.8 ± 14.0 floral units / m^2 (1 S.E., n = 8). The number of floral units of each species found in each of the 16 margins can be found in Supplementary Data 5 (included digitally alongside thesis). No correlation was found between the margin-level species richness and honeybee abundance (r_s = 0.332, *p* = 0.209 or wild bee abundance (r_s = 0.392, *p* = 0.134). Kings margins had a mean of 9.8 ± 0.8 (1 S.E., *n* = 8) and median of 10 entomophilous species at the margin level while NatReg margins had a mean of 7.0 ± 1.2 (1 S.E., *n* = 8) and median of 7 entomophilous species. This difference was not significant (W = 47, *p* = 0.123).

Removing the time taken to capture and label bees, the average time taken to walk each transect during the June/July 2019 bee surveys was 28 minutes, 17 seconds. A total of 623 bees were counted across the 16 margins. 415 of these were *Apis mellifera* (honeybees), 125 were *Bombus* species (bumblebees) and 83 were solitary bees. For the breakdown of the number of solitary bees, honeybees and bumblebees in each margin see Appendix 3.3. Kings margins had a mean of 48.9 ± 20.8 honeybees per margin (1 S.E., *n* = 8), while NatReg margins had a mean of 3.0 ± 1.5 honeybees per margin (1 S.E., *n* = 8). In terms of wild bees (bumblebee and solitary), Kings margins had a mean of 21.9 ± 4.3 (1 S.E., *n* = 8) and NatReg margins had a mean of 4.1 ± 1.4 (1 S.E., *n* = 8).

3.3.1 Bee abundance modelled according to the total nectar supply

The variables included in the Bee_{Hon} model can be found in Table 3.1, along with their significance values where relevant. For the Bee_{Hon} model, nectar sugar (mg/m^2/day) had a positive significant effect (t = 4.607, *p* = <0.001) on bee abundance. This relationship is shown in Figure 3.4. No significant effect of margin type or temperature was found for the Bee_{Hon} model. The pseudo-R^2 value indicates that the Bee_{Hon} model explained 61.9% of the deviance.

Margins 4 and 15 were identified by a Cook’s distance plot as influential points in the Bee_{Hon} model, likely because of the very large number of honeybees at both of these margins (see Table 3.2). When these margins were removed and the model was re-run (Bee_{Hon_out}), the margin level nectar sugar supply (mg/m^2/day) was no longer significant. Margin type in the Bee_{Hon_out} model was highly significant in explaining bee abundance (t = -2.508, *p* = 0.028) as can be seen in Table 3.3. The pseudo-R^2 value indicates that the

Bee_{Hon_out} model explained 40.4% of the deviance. Total honeybee abundance according to margin type once influential points were removed can be seen in Figure 3.5.

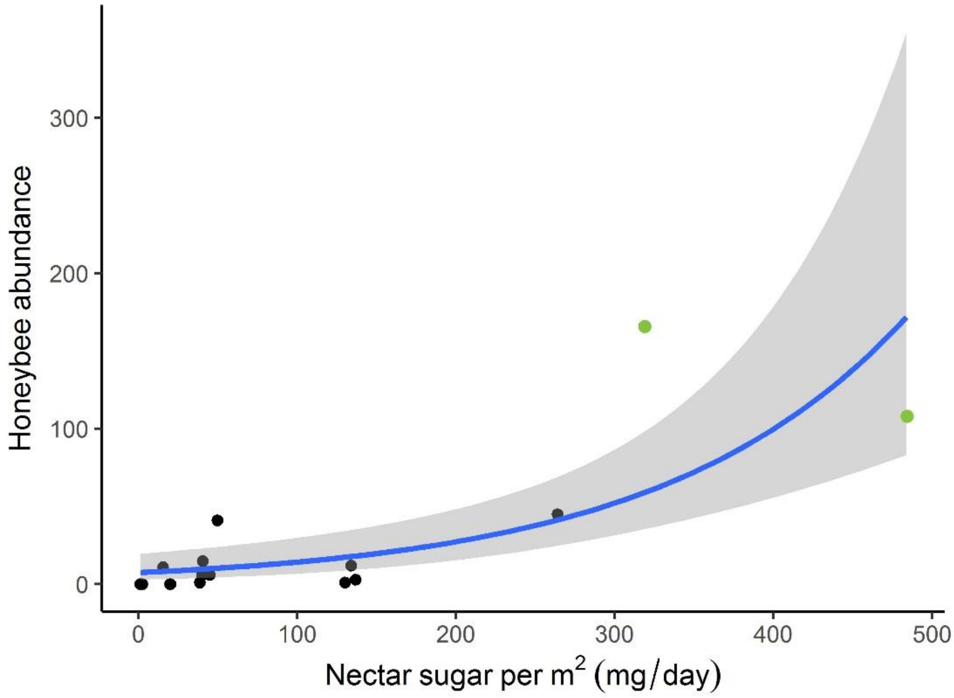


Figure 3.4 Honeybee abundance modelled as a function of nectar sugar (mg/m^2/day), including influential margins 4 and 15 (coloured in green).Each point represents a margin (n = 16). The blue line represents bee abundance modelled as a function of the nectar sugar supply (mg/m^2/day) using a generalised linear smooth function. The shaded area represents the standard error. The effect of nectar sugar (mg/m^2/day) upon bee abundance at the margin level was significant (t = 4.607, *p* = <0.001) in the Bee_{Hon} model.

Table 3.1 Explanatory variables included in the Bee_{Hon} model for honeybee abundance

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.011**	**0.489**	**NA**	**Kept in final model**	**0.001***
Nectar sugar (mg/m^2/day)	**0.006**	**0.001**	**Continuous**	**Kept in final model**	**<0.001***
Margin type (NatReg/Kings)	NA	NA	Categorical	6	NA
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant p-values marked with a (*) and marginally significant *p*-values (0.05 < "."< 0.1) are marked with (.).

Table 3.2 Nectar sugar supply (mg/m^2/day) in each margin and the proportion of all bees in each margin that were honeybees

Margin	Margin type	Nectar sugar (mg/ m^2/day)	Proportion honeybees (%)
1	NatReg	2.23	0.00
2	NatReg	1.07	0.00
3	NatReg	44.74	37.50
4	Kings	483.77	87.80
5	NatReg	38.61	50.00
6	Kings	263.98	78.95
7	NatReg	20.04	0.00
8	Kings	40.31	40.54
9	NatReg	39.97	85.71
10	NatReg	19.77	0.00
11	Kings	49.76	51.90
12	NatReg	15.36	55.00
13	Kings	130.07	7.14
14	Kings	136.73	13.64
15	Kings	318.56	79.43
16	Kings	133.81	48.00

The variables included in the original Bee_{Wild} models and their significance values where relevant are shown in Table 3.4. For the Bee_{Wild} model, there was no effect of nectar sugar or temperature upon total wild bee abundance (solitary bees and bumblebees). However, there was a significant effect of margin type upon bee abundance. Kings margins had a significantly greater number of wild bees than NatReg margins (means ± standard errors = 21.9 ± 4.3, and 4.1 ± 1.4, respectively n = 8, t = -3.853, p = 0.002). Wild bee abundance according to margin type can be seen in Figure 3.6. The pseudo-R^2 indicates that the Bee_{Wild} model explained 59.7% of the deviance. A Mann-Whitney U test also demonstrated that Kings margins produced a significantly higher (W = 63, p< 0.001) quantity of nectar sugar (mg/m^2/day) than NatReg margins (see Figure 3.7). Kings and NatReg margins respectively produced medians of 135.3 and 19.9 and means of 194.6 ± 53.4 mg/m^2/day (1 S.E., n = 8) and 22.7 ± 6.0 mg/m^2/day (1 S.E., n = 8) of nectar sugar.

Table 3.3 Explanatory variables included in the Bee_{Hon_out} model for honeybee abundance once margin outliers had been removed

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.970**	**0.308**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	6	NA
Margin type (NatReg/Kings)	**-1.872**	**0.746**	**Categorical**	**Kept in final model**	**0.028***
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	2	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	3	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'. Significant *p*-values marked with a (*).

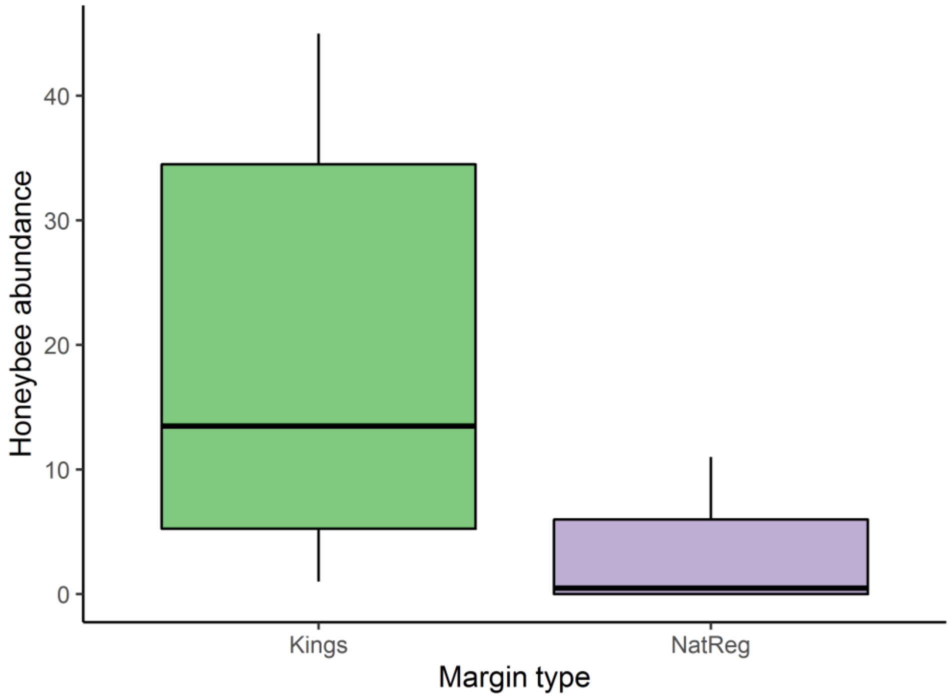


Figure 3.5 Honeybee abundance according to margin type (t = -2.508, p = 0.028) once influential margins (4 and 15) were removed in the Bee_{Hon_out} model. Kings margins are those sown with a grass/wildflower mix (n = 6) NatReg margins are those that have been allowed to regenerate naturally (n = 8). Note that each box represents the interquartile range, the horizontal line in the centre of the box represents the median value and the whiskers represent the highest and lowest values respectively.

3.3.2 Semi-natural habitat

The percentage of semi-natural habitat in 250 m radius buffers around each margin ranged between 0.0% and 30.9%. No difference (W = 18, p = 0.161, n = 8) was initially found between margin types (Kings and NatReg) when comparing the proportion of semi-natural habitat in 250m radius buffers (see Figure 3.8). However, when removing the outlier in the Kings mix that can be seen in Figure 3.8, the proportion of semi-natural habitat between the two margins was significantly different (W = 10, p=0.040). With the outlier removed, mean proportions of 2.1% ± 0.6% (1 S.E., n = 7) and 12.3% ± 4.0% (1 S.E., n = 8) were found surrounding Kings and NatReg margins respectively. A median proportion of 1.7% semi-natural habitat was found surrounding Kings margins and a

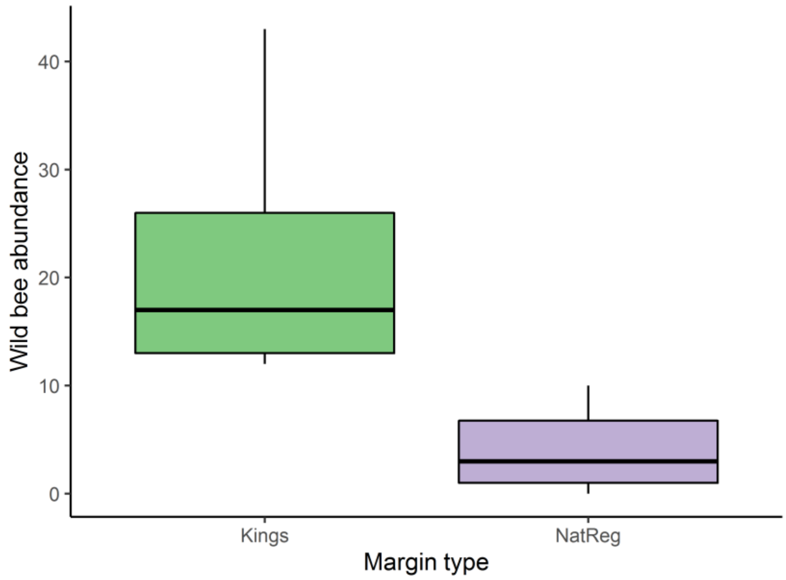


Figure 3.6 Wild bee abundance (bumblebees and solitary bees) according to margin type (n = 8). Kings margins are those sown with a grass/wildflower mix. NatReg margins are those that have been allowed to regenerate naturally. The difference in wild bee abundance between the margin types is significant (t = -3.853, p = 0.002). Note that each box represents the interquartile range, the horizontal line in the centre of the box represents the median value and the whiskers represent the highest and lowest values respectively.

median proportion of 10.4% was found surrounding NatReg margins when the outlier was removed. The area and proportion of semi-natural habitat surrounding each margin can be found in Appendix 3.4. The same pattern was found when comparing the proportion of semi-natural habitat in 500m buffers around each margin (see Appendix 3.5). No initial difference in the percentage of semi-natural habitat surrounding each margin was found between NatReg and Kings margins (W=15, p=0.083, n=8). Once again however, when the outlier seen in Figure S3.1 in Appendix 3.5 was removed from the Kings mix, the percentage of semi-natural habitat surrounding margins of each type was significantly different (W=9, p=0.029). There was a greater proportion of semi-natural habitat surrounding NatReg margins (Appendix 3.5).

Table 3.4 Explanatory variables included in the Bee_{Wild} model for wild bee abundance

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**3.085**	**0.173**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	5	NA
Margin type (NatReg/Kings)	**-1.668**	**0.433**	**Categorical**	**Kept in final model**	**0.002***
Mean temperature (°C)	NA	NA	Continuous	6	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

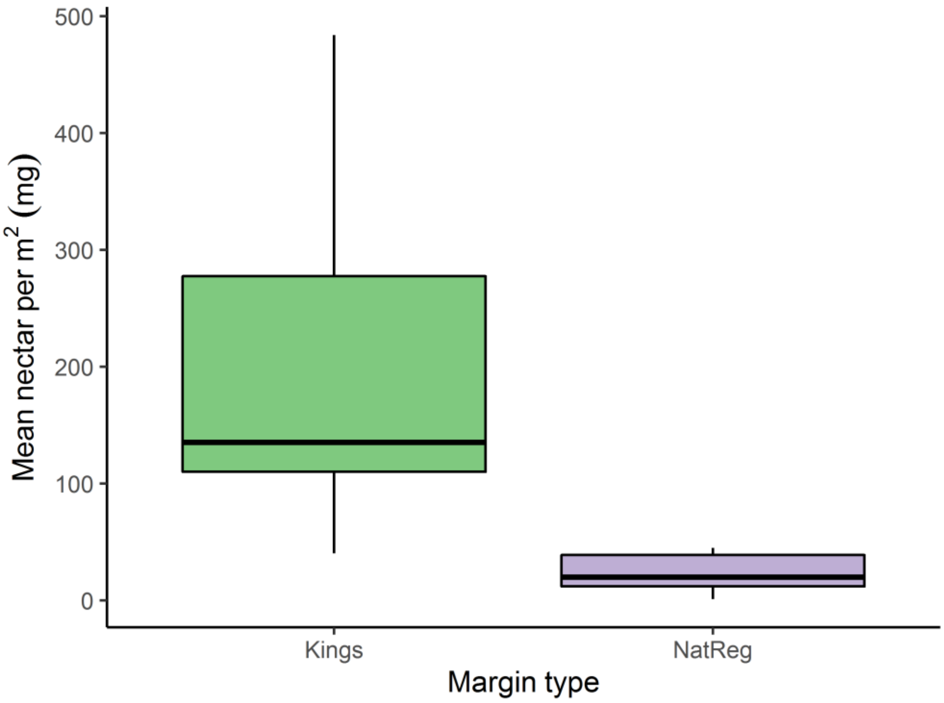


Figure 3.7 Mean total nectar sugar production (mg/m^2/day) according to margin type (n = 8). Kings margins are those sown with a grass/wildflower mix. NatReg margins are those that have been allowed to regenerate naturally. The difference between the two margin types is significant ($W = 63$, $p < 0.001$). Note that each box represents the interquartile range, the horizontal line in the centre of the box represents the median value and the whiskers represent the highest and lowest values respectively.

3.3.3 Bee abundance modelled according to the greatest nectar contributors

Nectar sugar supply at the margin level varied from 1.1 ± 0.3 mg/m^2/day (1 S.E., n = 10) to 483.8 ± 136.5 mg/m^2/day (1 S.E., n = 10). The entomophilous plant species producing the greatest proportion of this nectar sugar was *Centaurea nigra* which contributed 81.1% of the total margin nectar supply (See Figure 3.9). When comparing margin type, *Centaurea nigra* was the species that produced the greatest proportion of nectar sugar in Kings margins (90.6%), shown in Figure 3.9. *Rubus fruticosus* agg. (41.6%), *Cirsium arvense* (30.2%) and *Leucanthemum vulgare* (6.7%) together produced more than 75% of the total nectar sugar supply in NatReg margins. As the top nectar sugar contributors in Kings and NatReg margins respectively, the combined nectar sugar supply (mg/m^2/day) of these four species was subsequently included as a continuous variable ($nectar_{prox}$) in the Bee_{Hon_prop} and Bee_{Wild_prop} models.

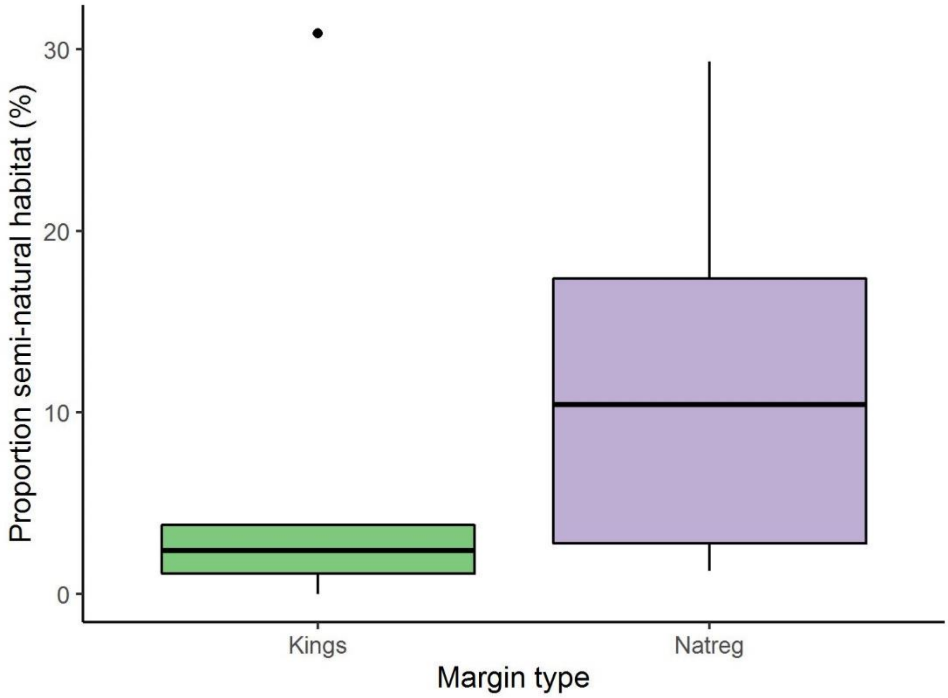


Figure 3.8 The proportion of semi-natural habitat in 250m buffers surrounding margin sections, according to each margin type (W = 18, *p* = 0.161, n = 8). Note that each box represents the interquartile range, the horizontal line in the centre of the box represents the median value and the whiskers represent the highest and lowest values respectively. The black point represents an outlier. If the outlier seen in the Kings mix is removed, the difference in the proportion of semi-natural habitat between the two margin types is significant (W = 10, *p*=0.040).

The $nectar_{prox}$ sugar supply ($mg/m^2/day$) explained honeybee abundance (t = 4.568, p <0.001) in the Bee_{Hon_prop} model before outliers were removed (see Table 3.5). Neither margin type nor mean temperature were significantly related to honeybee abundance. A pseudo-R^2 value of 61.7% was obtained for the Bee_{Hon_prop} model.

Two influential points (determined through Cook's distance plots) were removed (margin 4 and margin 15) and the Bee_{Hon_prop} model was run again ($Bee_{Hon\_propout}$). Once these influential points were removed, the $nectar_{prox}$ sugar supply ($mg/m^2/day$) no longer explained margin-level honeybee abundance. Instead, margin type was the only variable with a significant relationship (t = -2.508, p = 0.028) with honeybee abundance as can be seen in Table 3.6. This is therefore the same result as was achieved by removing outliers in the Bee_{Hon_out} model and, produces the same boxplot as can be seen in Figure 3.5 above. A pseudo-R^2 value of 40.4% was obtained for the $Bee_{Hon\_propout}$ model.

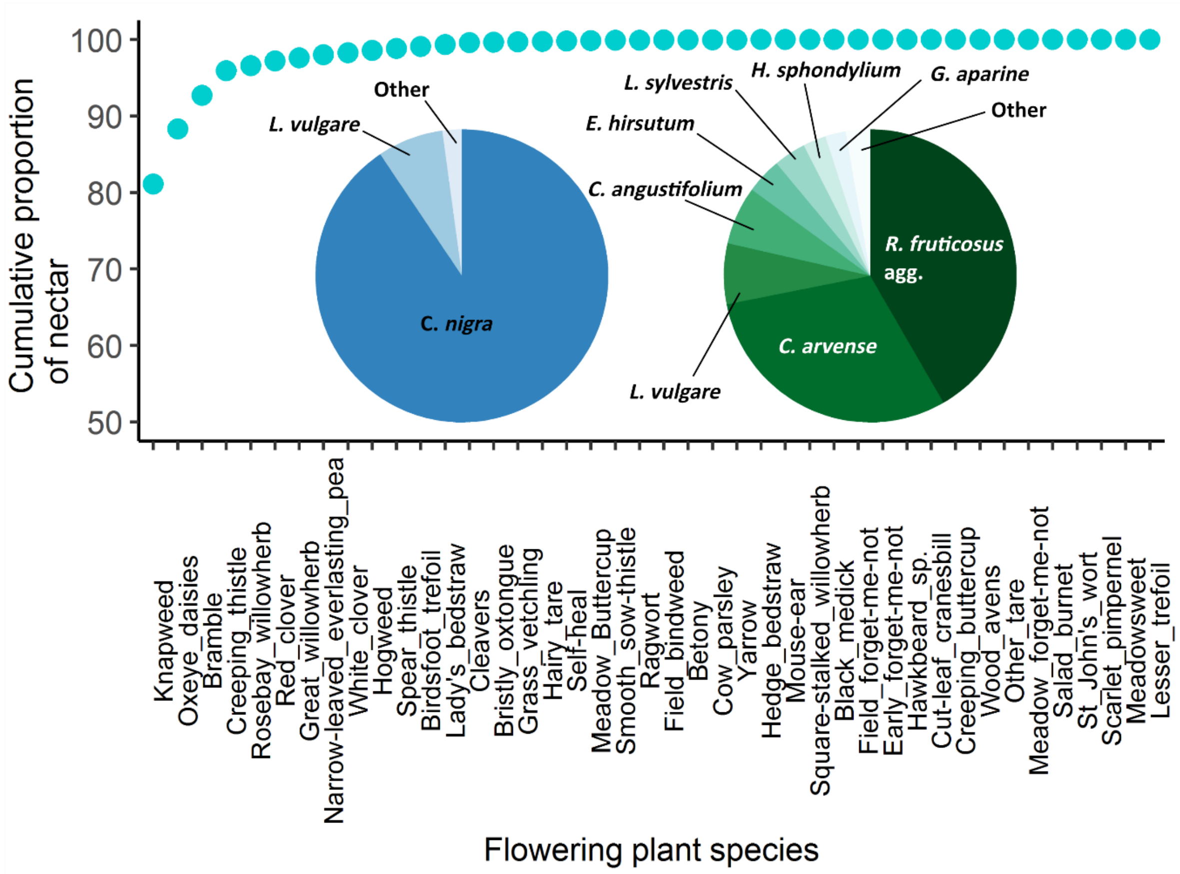


Figure 3.9 Cumulative frequency graph showing the proportional contribution of each entomophilous plant species to the total nectar sugar supply (mg/m^2/day) across the 16 margins. The pie charts underneath the cumulative frequency curve show the proportion of the total nectar supply being contributed by each plant species in Kings (blue) and NatReg (green) margins. Species are shown individually in the pie charts, unless they contribute less than 1% of the nectar contribution in each margin type respectively, in which case they are grouped into the 'other' category.

Table 3.5 Explanatory variables included in the Bee_{Hon_prop} model for honeybee abundance

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.047**	**0.486**	**NA**	**Kept in final model**	**0.001***
$Nectar_{prox}$ sugar ($mg/m^2/day$)[1]	**0.006**	**0.001**	**Continuous**	**Kept in final model**	**<0.001***
Margin type (NatReg/Kings)	NA	NA	Categorical	6	NA
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

[1]$Nectar_{prox}$ sugar supply ($mg/m^2/day$) is the combined supply for those species in each margin type that produce a minimum of 75% nectar in each margin type (*Centaurea nigra* in Kings margins and *Rubus fruticosus*, *Cirsium arvense* and *Leucanthemum vulgare* in NatReg margins).

Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant p-values marked with a (*).

In the Bee_{Wild_prop} model, wild bee abundance was significantly related to margin type ($t = -3.853$, $p = 0.002$) but no other variables, as can be seen in Table 3.7. This is similar to the result obtained with the Bee_{Wild} model, the latter using the total nectar sugar supply, rather than the $nectar_{prox}$ sugar supply and produces the same boxplot as seen in Figure 3.6 above. The pseudo-R^2 indicates that the Bee_{Wild_prop} model explained 59.7% of the deviance.

When comparing the $nectar_{prox}$ sugar supply (mg/m^2/day) between margin type, Kings margins were found to have a significantly greater nectar sugar supply than NatReg margins ($W = 62$, $p = 0.002$) as can be seen in Figure 3.10. Kings margins produced a mean of 191.1 ± 53.9 mg/m^2/day (1 S.E., $n = 8$) of nectar and median 134.0 mg/m^2/day, while NatReg margins produced a mean of 17.9 ± 5.6 mg/m^2/day (1 S.E., $n = 8$) and median of 13.1 mg/m^2/day.

3.4 Discussion

Overall, I found a positive correlation between honeybee abundance and total nectar sugar provision (mg/m^2/day) at field margin-level. These results support the first hypothesis. However, when carrying out standard model checks, margins 4 and 15 appeared as influential points in the Bee_{Hon} model. Upon removing these two influential points, the first study hypothesis was no longer supported. Instead margin type, rather than nectar sugar provision, was the main predictor of honeybee abundance.

The large numbers of honeybees in margins 4 and 15 are potentially a result of honeybee recruitment foraging strategies (e.g. Seeley et al., 1991), as discussed in detail below in Section 3.4.1. The potential for honeybee recruitment strategies to mask the relationship between floral resource availability and wild bee (bumblebees and solitary bees) abundance, was the basis for carrying out separate generalised linear models for wild bees (Bee_{Wild}). Margin type was the only variable to have a significant effect upon wild bee (solitary and bumblebee) abundance. Kings margins were found to have a higher wild bee abundance than NatReg. It is possible that the significantly higher nectar supply in Kings margins was leading to the higher bee abundance in Kings margins when compared to NatReg margins. However, nectar supply and semi-natural habitat proportion were

Table 3.6 Explanatory variables included in the $Bee_{Hon\_propout}$ model for honeybee abundance once model outliers were removed

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.970**	**0.308**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)[1]	NA	NA	Continuous	6	NA
Margin type (NatReg/Kings)	**-1.872**	**0.746**	**Categorical**	**Kept in final model**	**0.028***
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	2	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	3	NA
Margin type / Mean temperature	NA	NA	2-way interaction	4	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

[1]Nectar sugar supply (mg/m^2/day) is the combined supply for those species in each margin type that produce a minimum of 75% nectar in each margin type (*Centaurea nigra* in Kings margins and *Rubus fruticosus*, *Cirsium arvense* and *Leucanthemum vulgare* in NatReg margins).

Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant p-values marked with a (*).

Table 3.7 Explanatory variables included in the Bee_{Wild_prop} model for wild bee abundance

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**3.085**	**0.173**	**NA**	**NA**	**<0.001***
$Nectar_{prox}$ sugar (mg/m^2/day)[1]	NA	NA	Continuous	5	NA
Margin type (NatReg/Kings)	**-1.668**	**0.433**	**Categorical**	**Kept in final model**	**0.002***
Mean temperature (°C)	NA	NA	Continuous	6	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

[1]$Nectar_{prox}$ sugar supply (mg/m^2/day) is the combined supply for those species in each margin type that provide a minimum of 75% of the nectar sugar supply in each margin type (*Centaurea nigra* in Kings margins. *Rubus fruticosus* agg., *Cirsium arvense* and *Leucanthemum vulgare* in NatReg margins). Variables in bold are those that were kept in the final model. S.E. stands for 'standard error'. Significant *p*-values marked with a (*).

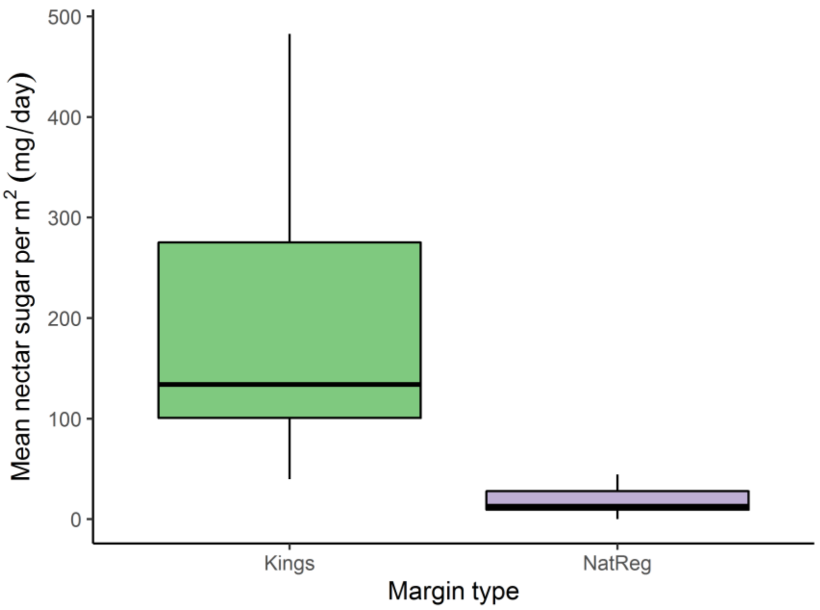


Figure 3.10 The combined nectar sugar supply (mg/m^2/day) provided by nectar$_{prox}$ species in each margin type (W = 62, *p* = 0.002, *n* = 8). *Centaurea nigra* is the species providing a minimum of 75% of the nectar sugar supply in Kings margins. *Rubus fruticosus* agg., *Cirsium arvense* and *Leucanthemum vulgare* are the species that together provide a minimum of 75% of the nectar sugar supply in NatReg margins. Note that each box represents the interquartile range, the horizontal line in the centre of the box represents the median value and the whiskers represent the highest and lowest values respectively.

confounding variables meaning that it was not possible to confirm this relationship. There are other differences between the margin types that could also be influencing this relationship as discussed in Sections 3.4.2 and 3.4.3.

In support of the second hypothesis, the results of the Bee$_{Hon_prop}$ and Bee$_{Wild_prop}$ models indicate that the entomophilous plant species that contribute the greatest proportion of the margin-level nectar sugar supply could be used as proxies for the total nectar sugar supply within bee abundance models. *Centaurea nigra* was the species contributing the greatest nectar sugar proportion in Kings mixes, and *Rubus fruticosus* agg. the species contributing the greatest proportion in NatReg margins. When using the combined nectar sugar supply values per margin for both of these species in the Bee$_{Hon_prop}$ and Bee$_{Wild_prop}$ models, the relationships were similar to those obtained using the total nectar supply in the Bee$_{Hon}$ and Bee$_{Wild}$ models. Once again, honeybee abundance appeared to be positively related to the nectar sugar supply, but upon removing margins 4 and 15 as outliers, only margin type had a significant effect. Similarly, only margin type had a significant effect upon wild bee abundance in the Bee_{Wild_prop} models, as was the case with the Bee_{Wild} models. Even when only considering nectar sugar produced by *C. nigra* and *R. fruticosus* agg., Kings margins produced a significantly higher quantity of nectar sugar ($mg/m^2/day$) than NatReg.

3.4.1 The influence of honeybee foraging recruitment strategies

Honeybee colonies selectively forage the most profitable nectar resource resulting in mass recruitment of foragers (Seeley et al., 1991). Waggle dances are the mechanism by which foraging honeybees recruit other foragers (Seeley et al., 1991). Both new and experienced honeybee foragers then follow waggle dances to identify new food sources (Biesmeijer and Seeley, 2005). Honeybees also have very large foraging ranges, with the mean foraging range for nectar found to be 1.4km in a study by Couvillon et al. (2015). Beekman and Ratnieks (2000) found a mean foraging range of 5.5km, with some bees foraging over 9.5km. In the latter study, the honeybee hive was located in the centre of the city of Sheffield and the bees were travelling the mean 5.5km in August to access flowering heather moors in close proximity to the city (Beekman and Ratnieks, 2000). The Beekman and Ratnieks (2000) study nicely demonstrated the effect of the recruitment foraging strategy (Seeley et al., 1991), with honeybees travelling a considerable distance to concentrate their efforts on abundant resources. The results of the study in this Chapter support the theory that honeybees selectively forage the most rewarding nectar resources and focus their recruitment efforts on rewarding flower patches. Margins 4 and 15 were identified by a Cook's Distance test as influential margins in the Bee_{Hon} model likely due to the high number of honeybees. Margins 4 and 15 were also the two margins out of the 16 producing the greatest quantity of nectar sugar (483.77 $mg/m^2/day$ and 318.56 $mg/m^2/day$ respectively), which likely would have made them very attractive to honeybee foragers.

It is therefore unlikely that margins 4 and 15 were outliers in an ecological sense, but rather that a high nectar sugar supply is likely to lead to high honeybee abundance in a non-linear way due to honeybee recruitment foraging strategies. A pseudo-R^2 value of 61.9% for the Bee_{Hon} model prior to the two influential margins being removed, compared to a pseudo-R^2 value of 40.4% once the two margins were removed, also support the suggestion that the nectar sugar supply was a likely driver of total bee abundance, albeit non-linearly.

While there was no significant relationship between the margin-level nectar sugar and wild bee abundance in the Bee_{Wild} model, a higher wild bee abundance was found in Kings compared to NatReg margins. This could still potentially be a result of the Kings margins producing a greater quantity of nectar sugar overall when compared to NatReg margins. However, it was not possible to confirm or deny this relationship as semi-natural habitat was a confounding variable that also differed between the two margin types, as I discuss in Section 3.4.2 below. The lack of a direct relationship between wild bee abundance and an increasing nectar sugar supply could also be partly influenced by the presence of honeybees. A reduced flower visitation rate by wild bees has been found in areas with honeybee hives/colonies present (Artz et al., 2011; Geslin et al., 2017; Bommarco et al., 2021). The presence of high numbers of honeybees in some margins could therefore potentially be suppressing the numbers of wild bees.

Nonetheless, margin 15 which was one of the two margins producing the greatest quantity of nectar sugar, also had the highest number of wild bees out of any margin. It is therefore possible that I simply didn't have enough margins in my study set with high nectar sugar values (mg/m^2/day) to demonstrate a direct positive relationship between margin-level nectar sugar supply and wild bee abundance.

3.4.2 Limitations - Habitat variability

The main aim of this study was to investigate the availability of nectar sugar at a margin level and the subsequent effect on bee abundance. The proportion of semi-natural habitat was therefore not included in the bee abundance models. Furthermore, given the small sample size (16 margins), including the proportion of semi-natural habitat within the modelling process would have led to over-parameterisation of the bee abundance models. However, the fact that semi-natural habitat can influence pollinator abundance, particularly in resource-poor agricultural landscapes (Lowe et al., 2021; Sheper et al., 2013), is acknowledged and is one of the limitations of this study.

I did compare the proportion of semi-natural habitat between margin types at the 250m and 500m spatial scales. NatReg margins were found to have a significantly higher proportion of semi-natural habitat than Kings margins at both spatial scales, making semi-natural habitat a confounding variable. As the opposite pattern between margin types was found for nectar sugar supply, i.e. NatReg margins produced a significantly lower quantity of nectar sugar than Kings margins, the two variables and their effects on bee abundance in each margin type could not be disentangled. The results are nonetheless interesting as wild bee abundance was lower in NatReg margins compared to Kings. It is possible that wild bees were being drawn away from NatReg margins if a higher nectar sugar supply and/or better quality nectar than was available in NatReg margins was present in the surrounding semi-natural habitat. Conversely, the higher wild bee abundance in Kings margins was potentially linked to the high nectar sugar supply in the margins drawing the bees away from the low proportion of semi-natural habitat surrounding Kings margins. The opposite effects of nectar sugar supply and semi-natural habitat could have potentially been creating an ecological contrast, accentuating the difference in bee abundance between the two margin types. If this was the case, it would support the findings of other studies that have shown sown nectar resources to be more important in already resource poor agricultural landscapes (Lowe et al., 2021; Scheper et al., 2013).

Similarly, as discussed in Section 3.4.1 above, when two influential margins were removed from the honeybee abundance models, only margin type had a significant effect on honeybee abundance. Kings margins had higher honeybee abundance than NatReg margins. This effect could again be due to the ecological contrast, i.e the accentuated difference in abundance as a result of the high nectar sugar supply and low proportion of semi-natural habitat in Kings margins and vice versa for NatReg margins. However, the proportion of semi-natural habitat surrounding margins is potentially less likely to influence honeybees when compared to wild bees. This is because they will selectively forage the most rewarding resources (Seeley et al., 1991) even over a large spatial scale (Beekman and Ratnieks, 2000), in theory making them a good study species when assessing the availability of nectar resources at the landscape level.

The presence of mass-flowering crops such as oilseed rape in the wider landscape can also influence bee abundance in margins (Le Féon et al., 2013). However, although *Brassica napus* was present at the study farm, it had finished flowering by the time of the bee surveys in June/July 2019 and, would therefore be unlikely to draw bees away from the field margins at that time of year (Holzschuh et al., 2011). Nonetheless, the fact that some margins had been adjacent to flowering *Brassica napus* earlier in the year is acknowledged. This could potentially still have influenced bee abundance as, the availability of resources at one point in time can affect future pollinator abundance (Guezen and Forrest, 2021; Timberlake et al., 2021).

3.4.3 Floral resources beyond nectar and their compatibility with different genera

In this study, I have focused on the relationship between nectar sugar availability and bee abundance. However, plants that are foraged for nectar aren't necessarily foraged for pollen. This is shown in a study by Goulson et al. (2005) for example, where Asteraceae species received 21.9% of nectar foraging visits by *Bombus* species, but only 2.2% of pollen foraging visits. Pollen quantity and its nutritional value, for example in terms of amino acid composition, macronutrient content or macronutrient ratio, varies enormously by flowering plant species (Tasei and Aupinel, 2008; Vaudo et al., 2016; Weiner et al., 2010) or even within flowering plant species (Roulston et al., 2000; Tasei and Aupinel, 2008). Potential differences in pollen quantity and nutritional value between NatReg and Kings margins could also be contributing to differences in bee abundance between the two margin types or, acting as a limiting factor that prevents a direct correlation between nectar sugar supply and wild bee abundance. The within-margin pollen availability and/or nutritional value and their inclusion as explanatory variables in bee abundance models alongside nectar, warrant further study.

However, it is not necessarily the case that adding pollen quantity and/or quality as variables within bee abundance models would improve the model fit. Timberlake et al. (2021) found that including pollen availability in their models investigating the relationship between nectar supply (g/km^2/day) and *Bombus terrestris* colony density (colonies/km^2) did not result in a greater model fit, likely due to a correlation between the nectar and pollen supply. A correlation between pollen and nectar would depend on the proportion of nectar-rich and pollen-rich species present in a habitat, which would vary according to environmental variables such as seed bank and management strategies (Pywell et al., 2011; Robinson and Sutherland, 2002).

The influence of floral resources at a particular location on bee abundance is also likely to vary by genera as indicated by Middleton et al. (2021). Overall pollinator abundance in field margins adjacent to potato crops was found to be higher in sown wildflower margins relative to controls and to have a positive relationship with floral cover (Middleton et al., 2021). However, when breaking the relationships down according to genera, a significant effect of floral cover upon *Andrena* was found, but no relationship was found between floral cover and other wild bee genera such as *Ceratina* or *Lassioglossum* (Middleton et al., 2021). By simply looking at floral cover, as do Middleton et al. (2021), or nectar availability, as is the focus of this Chapter, nuances in terms of the suitability of different entomophilous flowering plant species for different genera are not captured.

Bee genera vary according to their nutritional requirements (Ghosh et al., 2020; Vaudo et al., 2016; Vaudo et al., 2020), phenology (Hennessy et al., 2021; Ogilvie and Forrest, 2017), and morphological traits such as tongue length that are more or less compatible with different floral morphologies such as corolla depth (Basari et al., 2021; Klumpers et al., 2019). Breaking down the relationship between the margin-level nectar supply and bee abundance according to genera would therefore be an interesting next step for this research. Incorporating additional variables into bee abundance models, for example nectar sugar-supply from flowering forbs of a certain morphology, would help to tease apart some of the more nuanced relationships between bee abundance and nectar sugar supply.

3.4.4 Differences between margin types in resources beyond nectar

In addition to differences in terms of nectar production and other floral resources, there were other variables that could be influencing the significant difference in abundance of wild bees between NatReg and Kings margins. While the nesting resources/conditions required by many bee species is understudied (Antoine and Forrest, 2020), the nesting suitability of different habitats could have an influence upon bee abundance in a particular location (Roulston and Goodell, 2011). While many solitary bees excavate nests in the ground, other solitary bees and some *Bombus* species use cavities already available in a habitat such as abandoned rodent nests or hollow plant stems (Antoine and Forrest, 2020, Cane et al., 2007; Lye et al., 2012; Purvis et al., 2020). Antoine and Forrest (2020) review various ground conditions, ranging from ground cover to soil compaction, which could influence the suitability of a particular nesting location for nest-excavating bees.

It is possible therefore, that in addition to providing a greater supply of nectar, Kings margins also provided greater nesting opportunities for a variety of bee species when compared to NatReg margins. Kings margins consisted of sown grass and wildflower mixes, which potentially had more exposed ground for ground-dwelling bees than the very thickly vegetated NatReg margins. The latter, despite sometimes having areas of long grassy vegetation, often consisted of swathes of *Urtica dioica*, *Rubus fruticosus*, or willowherb species such as *Epilobium hirsutum* with little ground exposed. While many solitary bees (e.g. *Halictus rubicundus*) readily nest in bare ground (Gregory and Wright, 2005; Maher et al., 2019; Potts et al., 2005), a citizen-science based study by Maher et al. (2019) found that the majority of nest aggregations for some solitary bee species such as *Colletes hederae* were found in grassy areas. The grassy habitat in Kings margins would also be suitable for *Bombus* species that nest in grassy patches, for example *Bombus pascuorum* (Lye et al., 2012).

3.4.5 Floral resources according to margin type: the importance of management

The finding that the Kings margins had a significantly greater abundance of wild bees when compared to NatReg margins is similar to Meek et al. (2002), who found that butterfly and bumblebee abundances were significantly greater ($P<0.001$ and $P<0.01$ respectively) in margins sown with a grass/wildflower mix than in naturally regenerated margins. Contrary to my results, Pywell et al. (2005) found no significant difference in bumblebee abundance or species richness between margins allowed to regenerate naturally and those with sown wildflower mixes. Carvell et al. (2004) found that bumblebee abundance in different margin types depended on year. In year one of the study, significantly greater bumblebee numbers ($p<0.01$) were found in margins sown with wildflowers than in naturally regenerated margins. In the second year of the study however, the greatest number of bumblebees was recorded in naturally regenerated margins, although this difference was not significant when compared to those sown with wildflowers. This difference was attributed to the fact that the naturally regenerated margins had a large abundance of *Cirsium vulgare* flowering in the second year of the study (Carvell et al., 2004).

Naturally regenerated margins do not rely on the enhancement of floral resources. Their floral composition is therefore likely to vary considerably from farm to farm, according to both the existing seed bank and management (Carvell et al., 2004; Pywell et al., 2005). These factors perhaps account for some of the variability between different studies, in terms of the relative abundance of pollinators between naturally regenerated margins and those sown with a wildflower mix (Carvell et al., 2004; Meek et al., 2002; Pywell et al., 2005). Pywell et al. (2005) for example, note the relative diversity of the plant species in the naturally regenerated margins at their study farms, linked to a specific management regime employed to provide appropriate conditions for rare arable plants and which involved yearly cultivations. This encouraged the growth of *Cirsium* species, which accounted for the majority of the foraging resource in naturally regenerated margins (Pywell et al., 2005). The management regime employed by Pywell et al. (2005) is considerably different to that applied at the farm in this study which involved allowing scrubby vegetation such as *Rubus fruticosus* agg. to grow and then cutting it back every few years and which could account for the lower nectar resource in NatReg margins compared to the sown Kings wildflower margins.

Several important points regarding the management of field margins in intensively-farmed arable landscapes are subsequently raised. Firstly, a low floral richness for some naturally regenerated margins could be attributed to the fact that the seed bank densities of farmed arable landscapes have declined considerably over the course of the 20th Century (Robinson and Sutherland, 2002). A low floral species richness is less likely to be an issue with sown wildflower margins where the seed bank is essentially being replenished. Carvell et al. (2004) note also the greater consistency in resources provided through sown wildflower margins on a yearly basis, when compared to naturally regenerated margins. In agricultural regions where the existing seed bank is already poor, relying on naturally regenerated margins alone to provide pollinator communities with all of their floral resource requirements would be a poor strategy and, supplementing floral resources via sown wildflower mixes would be preferable.

In this study, floral species richness was not found to vary between margin type but, the nectar sugar supply was found to be significantly lower in NatReg margins compared to Kings. In other arable farming systems where naturally regenerated margins are nectar-poor, supplementing floral resources via sown wildflower mixes would also be an important strategy. As floral species richness and nectar supply at the margin level are not necessarily correlated, as was the case in this study, assessing the variability in the margin-level nectar sugar supply between naturally regenerated margins across different regions or farms would be a useful area for future research.

Where naturally regenerated margins are established as an agri-environment intervention, changing management practices could still enhance the floral abundance, richness and subsequent resource availability. Where naturally regenerated margins consist in large part of scrubby vegetation such as *Rubus fruticosus*, such as the ones at the farm in this study, cutting regime could have an influence upon floral unit abundance. This is evidenced by Staley et al. (2012), who demonstrate that flower abundance is 2.1 times greater when cutting of *Crataegus monogyna* hedgerows is implemented on a 3-yearly basis rather than every year.

3.4.6 The influence of total nectar sugar and nectar sugar proxies upon bee abundance

Traditionally, variables such as flower abundance or floral cover have been used as proxies for floral resources (Szigeti et al., 2016). However, there is not necessarily a linear relationship between floral abundance and floral resources such as pollen and nectar (Purvis et al., 2020) or between flower-rich habitat and pollen/nectar resources (Timberlake et al., 2021). As reviewed in Section 3.1, studies have more recently started to demonstrate the important link between nectar and bee abundance at the regional and farm levels (Jachuła et al., 2021; Timberlake et al., 2019). The significant difference in the mean nectar sugar supply between arable field margin types in this study, as well as the variability in nectar sugar supply within the same margin type (varying by 10-fold in the Kings margins for example), demonstrates the need to consider the within- and between-habitat floral resources in future studies.

At the margin-level, the honeybee abundance across arable field margins (eight naturally regenerated and eight sown with a wildflower mix) initially appeared to be related to the quantity of nectar sugar produced. This was likely driven by honeybee recruitment foraging strategies as discussed in detail in Section 3.4.1. Once two influential margins were removed from the model (Bee_{Hon_out}), margin type was the only variable that was highly significant in explaining honeybee abundance. Margin type was also the only variable with a significant effect upon wild bee abudance in the Bee_{Wild} model.

The Bee_{Hon_prop} and Bee_{Wild_prop} models included the margin-level nectar sugar provision (mg / m^2) of those species contributing the greatest proportion of nectar sugar in each margin type, as a proxy for the total nectar sugar supply. The relationship between bee abundance and the proxy nectar sugar supply followed the same pattern as the original Bee_{Hon} and Bee_{Wild} models. There was a significant effect of the proxy nectar sugar supply on honeybee abundance but, this was being driven predominantly by two influential margins (4 and 15) with high nectar sugar supplies that were likely attracting high numbers of honeybees due to honeybee recruitment strategies (Seeley et al., 1991). Once the two influential margins were removed in the $Bee_{Hon\_propout}$ model, margin type was the only variable with a signifjcant effect on honeybee abundance. In the Bee_{Wild_prop} model, margin type was again the only variable with a significant effect upon wild bee abundance. I outlined the potential reasons behind this in Sections 3.4.1, 3.4.2, 3.4.4 and 3.4.5 above.

The results do suggest that remote sensing programmes could focus initially on mapping key nectar-rich flowering plant species that are the greatest contributors to the nectar supply within agricultural field margins, as a starting point for understanding the spatial availability of nectar resources for pollinators. This is one of the key aims of this thesis, which I started to address in Chapter 2. I used remotely-sensed multispectral imagery to determine the accuracy with which five nectar-rich flowering plant species could be classified.

It should be noted however, that the floral and bee abundance surveys in this study were only carried out in June/July. The composition of key nectar-rich flowering plant species and the subsequent nectar sugar supply varies with time of year (e.g. Timberlake et al., 2019). Further research would be needed to determine which flowering plant species are the key nectar-contributors within different margin types throughout the year, so that a set of flowering plant species to map using remote-sensing technology could be prioritised.

Subject to the accuracy with which nectar-rich flowering plant species can be mapped using high-resolution remote sensing technology, maps outlining the spatial and temporal availability of nectar sugar in arable field margins could subsequently be produced. Understanding the baseline spatial and temporal availability of nectar-rich pollinator foraging resources could allow resource gaps to be filled. This is the focus of the following PhD Chapter.

Chapter 4

How accurate are classifications of floral resources from Unmanned Aerial Vehicles (UAVs)?

4.1 Introduction

In Chapter 1 I discussed the issues surrounding pollinator decline (Goulson et al., 2015; Potts et al., 2010; Potts et al., 2016), as well as the suggestions for addressing these. Part of the solution is to increase the availability and diversity of food and nesting resources, such as nectar/pollen or suitable nesting habitat (Baude et al., 2016; Carvell et al., 2017; Pywell et al., 2005; Scheper et al., 2013). The focus of this PhD project has been upon the availability of nectar sugar within arable landscapes, due to its function as an energy source for pollinators (Brodschneider and Crailsheim, 2010; Willmer et al., 2011). Remote-sensing nectar-rich flowering plant species is also the focus of this Chapter.

In order to mitigate declines and set new pollinator habitat management targets, a baseline understanding of the nectar sugar resource already available is required. While this has traditionally been acquired through quadrat surveys of flower densities on the ground, remote sensing potentially offers an exciting new route for obtaining a baseline at much larger scales and as an exact spatial representation of the floral resource on the ground (Galbraith et al., 2015; Willcox et al., 2018). Much of the pollinator nectar sugar supply comes from floral units of sub-centimetre to several centimetres in size. It is only recently, with the rising availability of very high spatial resolution (in the range of several centimetres) remote-sensing technologies, that contemplating mapping such floral resources remotely has become feasible (Carl et al., 2017, Chen et al., 2009 and Horton et al., 2017).

Chapter 2 demonstrated that five key nectar-rich flowering plant species in a UK agricultural landscape could be mapped using very high resolution (3cm and 7cm) multispectral aerial imagery (overall accuracies ranging between 92.3-98.7%), with a range of user's and producer's accuracies (ranging between 76.1-98.3% and 52.0-95.3% respectively). In this Chapter, I determine whether high-classification accuracies can be obtained using unmanned aerial vehicles (UAVs). The use of UAVs is described in more detail in Section 4.1.1. Various 'hard' classification techniques are available including parametric classifiers such as maximum likelihood and non-parametric classifiers such as random forest (e.g. see Belgiu and Drăguţ, 2016; Lu and Weng, 2007). Both of these classifiers are used in this study. I describe them in more detail in Section 4.1.2.

In Chapter 2, *Crataegus monogyna* had low user's accuracies, likely lower due to the presence of similarly-coloured synchronously flowering species. However, as the remote-sensing of the floral component of nectar-rich flowering plant species has not been extensively studied, we do not know which flowering plant species commonly found in UK agricultural landscapes can be mapped separately from one another. In this Chapter, I therefore determine whether flowering plant species with similarly-coloured synchronously-flowering species can be classified individually from one another or whether some species are better classified as a single classification category. I describe this in further detail in Section 4.1.3.

When using traditional 'hard' classification techniques such as maximum likelihood (employed in Chapter 2 and in this Chapter) and random forest (employed in this current Chapter), an image pixel is allocated to one of a number of different classification categories. In this study for example, one classification category would be the floral component of a nectar-rich flowering plant species of interest. From the final classification, the area classified (m^2) as the floral component of a focal flowering plant species can subsequently be derived. However, it is not known how many floral units on the ground are represented by this classified area. This is a key piece of missing information when estimating the nectar sugar supply per unit area, which is derived from published data available for the number of flowers per floral unit (Baude et al., 2015b) and the nectar sugar supply for each flower (µg/flower/day; Baude et al., 2015a). A final aim of this study therefore, is to determine whether there is a correlation between the area classified as the floral component of a flowering plant and the number of floral units on the ground.

4.1.1 The application of unmanned aerial vehicle imagery in agricultural systems

In Chapter 2, I researched the accuracy with which nectar-rich floral resources within an agricultural landscape could be classified using airborne imagery obtained via a manned aircraft. Unmanned Aerial Vehicles (UAVs) are another platform used frequently within the agricultural sector. Through the detection of metrics such as crop cover, leaf water content and so on, UAVs can be used for crop monitoring (Daponte et al., 2019; Norasma et al., 2019). UAVs are consequently hugely beneficial when adopting an on-farm policy of precision agriculture, as they allow for targeted management of a crop (Daponte et al., 2019; Delavarpour et al., 2021; Norasma et al., 2019). Agrochemical inputs can be applied where they are specifically required, rather than across an entire field, which can lead to a reduction of inputs and greater productivity (Daponte et al., 2019).

A number of studies have started using UAV imagery to map flowers of individual plant species, for example in invasive species mapping (Carl et al., 2017) or for mapping the flowers of fruit trees within an orchard context (Horton et al., 2017). As far as I am aware however, no studies have used UAV imagery to map the fine-scale floral resources available to pollinators and other wildlife within an arable field margin context, as I do here. If it is possible to map nectar-rich floral resources within arable field margins using UAV imagery, it would be feasible for farmers to extend the monitoring of cropped fields into the margins / other boundary habitats. This could allow for a baseline assessment of floral resources and their continued monitoring, so that targeted management decisions can be made for the benefit of pollinators and other wildlife. As noted in Chapter 2, a baseline assessment would also allow any measures implemented as part of an agri-environment scheme to be assessed in terms of their outcomes, i.e. the resulting additional floral resources obtained via particular interventions, and monitoring these outcomes over time (Tansey et al., 2009). Initially measuring and then monitoring biodiversity outcomes could become more relevant as agri-environment schemes shift towards a ‘payment-by-results’ approach, where farmers and land managers are paid for achieving particular biodiversity targets, rather than for the process itself (Chaplin et al., 2021).

4.1.2 Maximum likelihood and random forest classifications

In Chapter 2, I used a maximum likelihood (ML) classifier thanks to its availability and ease-of-use through various software packages (Lu and Weng, 2007). This would facilitate its application by farmers and other agricultural businesses directly involved in land management. Furthermore, the ML classifier has been widely used to produce accurate maps to answer various ecological questions. Everitt et al. (2007) for example, used ML to map invasive *Colocasia esculenta* (L.) Schott along the Rio Grande river with user's accuracies of 100% across three sites and producer's accuracies of 83.3-100.0%. Ruwaimana et al. (2018) demonstrated that drone imagery with a 2.8cm resolution could be used to map plant species and non-plant features within mangrove ecosystems. The study obtained mean overall classification accuracies of 77.6 ±1.3% and 90.0 ±1.9% using pixel-based ML classification algorithms with 10 and 6 land use / land cover categories respectively.

Non-parametric machine-learning approaches are alternative classifiers that have the advantages of having greater flexibility than parametric classifiers and of not relying on normally distributed data (Belgiu and Drăguţ, 2016; Gómez et al., 2016; Lary et al., 2016; Lu and Weng, 2007). One machine-learning approach is the random forest (RF) classifier. The RF classifier is known as an 'ensemble' approach, whereby multiple classification category prediction trees are grown using a random selection of input data. Each tree votes for a classification category based on its input data and the final classification category is determined by the greatest number of votes (Breiman, 2001 and Belgiu and Drăguţ, 2016). Since its inception in 2001 (Breiman et al., 2001), the RF classifier has increasingly been used in remote sensing applications, thanks to its ability to choose the variables best suited for distinguishing between different classification categories (Belgiu and Drăguţ, 2016; Gómez et al., 2016). Use of the RF classifier has extended to applications in the fields of conservation and ecology, for example to estimate rates of deforestation (Grinand et al., 2013).

As the use of RF and other machine-learning approaches expand, they are no longer only available via software programs that are either costly or that require extensive coding knowledge (Belgiu and Drăguţ, 2016). For example, version 7 of the Semi-automatic classification plugin (Congedo, 2021) that is available in QGIS (QGIS, 2021), now offers RF as a classification option. In light of this rapid development, in this study both ML and RF classifiers are applied to the imagery obtained of the study area.

4.1.3 Mapping species of similar colours in the visible range

Chapter 2 demonstrated that species flowering in agricultural hedgerows and field margins with no similarly-coloured, synchronously flowering species, could be mapped with very high user's and producer's accuracies. For example, *Prunus spinosa* flowering in the hedgerow in March had a user's accuracy of 98.3% and a producer's accuracy of 87.5% in classifications with a 3cm spatial resolution. On the other hand, *Crataegus monogyna* flowering in the hedgerow in May had lower user's and producer's accuracies (77.8% and 65.6% respectively). This was because the similarly coloured *Anthriscus sylvestris* was also flowering. However, it is surprising that with *A. sylvestris* flowering synchronously, that user's and producer's accuracies for *C. monogyna* were not even lower than they were. This could be linked to differences in flower density. While *C. monogyna* often flowers very densely within a hedgerow, *A. sylvestris* has tiny flowers packed loosely in umbels through which you can usually see green background vegetation.

As well as flowering density, flower species can vary according to other features such as petal structure and thickness, which could also potentially influence electromagnetic reflection (van der Kooi et al., 2019; Vignolini et al., 2012). Differing reflectance spectra linked to the non-pigment biochemical compositions (e.g. concentrations of water, cellulose, etc.) of vegetation from the leaf to the canopy level have been used to distinguish between different plant species (Kokaly et al., 2009). There is no reason to assume that the non-pigment biochemical composition of the floral component of plant species does not also vary, including in the infra-red range. The spectral signature of the floral component of plant species is therefore not necessarily only linked to the colour of individual floral units, despite their colour superficially appearing similar to the human eye. In this study, I determine whether nectar-rich flowering plant species can be classified separately from co-flowering species with similar floral colours, when using multispectral 3cm unmanned aerial vehicle imagery. Control species of a similar colour to and synchronously flowering with target nectar-rich species are included in the classification training and accuracy assessment process.

As noted in Chapter 2, *Cirsium* thistles (*C. arvense* and *C. vulgare*) were flowering synchronously with *Centaurea nigra* at the study farm in 2019. The floral units (following the definition of Carvell et al., 2007) of both *Cirisum* species and *Centaurea nigra* are capitulums that share similar floral unit morphologies as they consist predominantly of densely-packed disc florets (Stace, 2010), although some forms of *C. nigra* do also have ray florets, as can be seen in Figure 4.3 (d). In the Floral Reflectance Database (FReD, 2021), *Cirsium arvense* is defined as being 'pink' in human colour. While *Centaurea nigra* is not present in the database, other *Centaurea* species that are very similar in appearance such as *C. jacea* and *C. nigrescens* are present and these species are also defined as being pink/violet as perceived by humans (FReD, 2021). I therefore use these two species as a case study for determining whether co-flowering species that look similar to the human eye on the ground are more accurately amalgamated into a single classification category rather than individually.

4.1.4 Research questions

As reviewed in Section 4.1.3, there is little knowledge surrounding which floral components of synchronously flowering entomophilous species can be classified separately from one another when their flowers share similar colours in the visible wavelength range. This study aims to address whether two of the most nectar-rich flowering plant species within the field margins of a UK-based arable farm can be classified separately from synchronously flowering plant species with similarly-coloured floral components using two types of classifier (maximum likelihood and random forest). Two of the flowering plant species at the study farm that produce the greatest quantity of nectar sugar (mg / floral unit / day) are *Centaurea nigra* and *Leucanthemum vulgare*. Specifically I ask:

4.) 'Can 3cm resolution UAV imagery be used to accurately classify the floral component of *Leucanthemum vulgare* and *Centaurea nigra* and distinguish these species from control species with floral components of similar colours?

5.) ‘Can high classification accuracies for *Leucanthemum vulgare* and *Centaurea nigra* be achieved when using both maximum likelihood and random forest classifiers?’

As well as being similar colours, some the floral units of some species such as *Cirsium arvense* and *C. nigra* are also structurally similar. As noted in Section 4.1.3, the floral component of species such as these could potentially be more accurately classified as one combined classification category. I ask:

6.) ‘Are classification accuracies improved when combining *Cirsium arvense* and *Centaurea nigra* into one *Cirsium* / *C. nigra* classification category as opposed to classifying them individually?’

In order to turn the area classified as the floral component of a particular flowering plant species into an estimate of the actual nectar sugar supply on the ground, the number of floral units represented by the classified area needs to be determined. The combined *Cirsium*/*Centaurea nigra* classification category, hereafter termed $\text{Thist}_{\text{group}}$, is subsequently used as a case study for determining whether the area classified via remote sensing surveys is correlated with the number of floral units on the ground. I ask:

7.) ‘Is the area (m^2) classified as $\text{Thist}_{\text{group}}$ correlated with the number of floral units of $\text{Thist}_{\text{group}}$ on the ground (floral units / m^2)?’

4.2 Materials and Methods

4.2.1 Study site and target nectar-rich flowering plant species

This study was carried out at a conventional arable farm in Northamptonshire, UK. The farm was between two central locations, approximately 7.98km apart (co-ordinates for the approximate centre of location 1 = 52°18'9"N, 0°45'41"W and co-ordinates for the approximate centre of location 2 = 52° 13' 51"N, 0° 46' 18"W). Further details regarding the study farm can be found in Chapter 2, Section 2.2.1. The majority of fields were surrounded by 6m wide margins that were either allowed to regenerate naturally or that had been planted with pollinator wildflower mixes from three of the main pollinator seed providers in the UK: Emorsgate seeds (EM1), Limagrain (AWF4) and Kings Crops. These mixes varied slightly but contained many of the same species. The full list of species included as part of the Kings Crops mix can be found in Appendix 3.1, the species included in Emorsgate EM1 mix can be found in Appendix 2.1, and the Limagrain (AWF4) mix can be found in Appendix 4.1.

The study site included $Area_1$, an area of ~0.34 km^2, which was used for gathering ground-truth data for use within the classification training and accuracy assessment processes (see Figure 4.1). $Area_1$ covered four fields and their respective margins and a meadow (field 3 in Figure 4.1) planted with a wildflower mix designed with Emorsgate to recreate a native wildflower meadow. Many flowering plant species in the meadow overlapped with those included within the sown wildflower margins such as *Centaurea nigra*, *Leucanthemum vulgare* and *Achillea millefolium*. While the meadow was used as an area for gathering ground-truth data, only those species also found in the sown wildflower margins were included as part of the study.

The study site also included 16 margin sections, eight naturally regenerated and eight sown with a Kings Crops wildflower mix (see Appendix 3.1), the latter hereafter termed 'Kings'. These were the same 16 margin sections used for carrying out floral surveys and bee abundance surveys as described in Chapter 3 (see Chapter 3, Section 3.2.1 for margin locations). Margin sections were approximately 105m long and 6m wide. Each of the 16 margin sections were used for addressing research question 7.

As in Chapter 2, only floral species growing abundantly within sown wildflower margins across $Area_1$, were selected for inclusion as the main flowering plant species classification categories. This was so that adequate ground-truth data were available at a later stage for classification training (50 pixels of data) and verification (64 pixels of data). 'Abundant' species were estimated by sight as having multiple clusters of floral units within four 100m X 1m plots across a minimum of four different fields. Flowering plant species growing abundantly across the study area and sown as part of a wildflower mix were ordered from highest to lowest according to their nectar sugar production values per floral unit (µg / floral unit). Nectar production values per floral unit were obtained by multiplying the mean nectar sugar production per flower (Baude et al., 2015a) by the mean number of flowers per floral unit (Baude et al., 2015b). A floral unit was defined as a flower or a stem with multiple flowers that a bee can walk rather than fly between (Carvell et al., 2007).

Figure 4.1 Area$_1$ where training and verification ground-truth data were collected is outlined in blue. Numbers refer to the field number. Field number 3 is the meadow. See Figure 1.3 and Figure 1.4 in Chapter 1 for context of where Area$_1$ sits relative to the rest of UK and the rest of the study area.

On both image acquisition dates (13th and 30th July 2020), *Centaurea nigra* and *Leucanthemum vulgare* constituted the two flowering plant species sown as part of a wildflower margin mix that produced the greatest quantity of nectar per floral unit (according to Baude et al., 2015a and Baude et al., 2015b). They were therefore selected as the two target flowering plant species classification categories (see Table 4.1). *Cirsium arvense* was also abundant across the study site but was not part of any of the sown wildflower mixes.

Table 4.1 All flowering plant species included as classification categories and their nectar sugar values at the flower and floral unit level

Latin name	Vernacular name	Mean nectar sucrose content (µg/flower/day ± SD)[1]	Mean number of flowers in floral unit[2]	Nectar sucrose per floral unit (µg/floral unit/day)[3]
Centaurea nigra	Common knapweed	199.0 ± 152.2	53.8	10705.7
Chamerion angustifolium	Rosebay willowherb	941.6 ± 561.8	1.0	941.6
Cirsium arvense	Creeping Cirsium	76.2 ± 58.2	85.8	6539.7
Cirsium vulgare	Spear Cirsium	76.5 ± 93.0	195.2	14932.8
Leucanthemum vulgare	Ox-eye daisy	15.8 ± 11.6	135.2	2137.5
Daucus carota	Wild carrot	7.4 ± 9.6	32.7	241.98
Epilobium hirsutum	Great willowherb	323.5 ± 194.4	1.0	323.5
Achillea millefolium	Yarrow	7.6 ± 7.5	5.6	42.3

[1] Baude et al. (2015a), [2]Baude et al. (2015b), [3] Mean nectar sucrose per flower from Baude et al. (2015a) multiplied by mean no. flowers per floral unit from Baude et al. (2015b). Note: SD stands for standard deviation.

4.2.2 Imagery acquisition

HexCam, a company that specialises in acquiring and processing unmanned aerial vehicle (UAV) imagery, acquired the imagery for this study (HexCam, 2022). Two Sentera AGX710 sensors attached to a DJI Phantom UAV were used to capture data on 13th July 2020 and 30th July 2020. The corresponding imagery sets are hereafter called UAV_{Set1} and UAV_{Set2}. The UAV was flown at a height of approximately 100m to capture imagery of $Area_1$ and the 16 EM1 margin sections with a ground-sampling distance as close to 3cm as possible (2.95cm and 3.00cm for UAV_{Set1} and UAV_{Set2} respectively). The first Sentera sensor had optimized focal lengths of 5.309mm and 5.431mm for UAV_{Set1} and UAV_{Set2} respectively, and captured data in the red, green, blue (RGB) bands. The second sensor had optimized focal lengths of 5.324mm and 5.447mm respectively for UAV_{Set1} and UAV_{Set2} datasets and captured red-edge and near-infrared data.

Weather conditions recorded automatically by the UAV platform on 13th July 2020, the date of imagery acquisition for UAV_{Set1}, were 100% cloud cover with a 4.6 m/s wind speed. Weather conditions recorded automatically by the UAV platform for the UAV_{Set2} imagery capture on 30th July 2020, were clear (28% cloud cover) and 3.2m/s wind speed. The difference in cloud cover between the two image dates was not an issue as I was not comparing the two images to one another.

Data pre-processing was carried out by Hexcam using Pix4D. Noise filtering and surface smoothing were applied to the data and an orthomosaic was produced. Data were collected using a WGS 84 (EGM96 Geoid) coordinate reference system (CRS) but were re-projected to an OSGB 1936/British National Grid CRS.

4.2.3 Gathering ground-truth data for *Centaurea nigra* and *Leucanthemum vulgare*

For UAV_{Set1}, four ground-truth plots both containing *Centaurea nigra* and *Leucanthemum vulgare* were established. Each of these were located within separate fields across $Area_1$ (see Figure 4.2a). These plots consisted of 10m^2 rectangular areas marked out by white ground control point (GCP) boards. Each site was further divided with smaller GCP boards into 1m^2 sub-plots. Photos and floral unit counts were taken for each sub-plot. Based on their respective locations within the photos, the location of clusters of floral units within the UAV imagery could be determined (see Figure 4.3).

(a) (b)

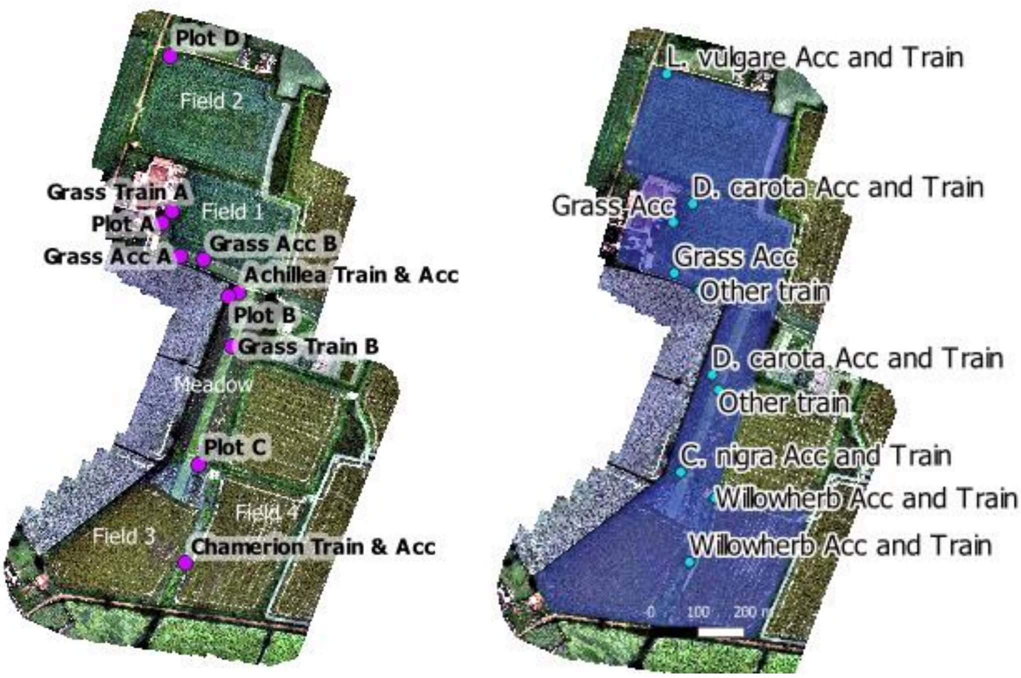


Figure 4.2 (a) Ground-truth plots for UAV$_{Set1}$. Plots A, B, C and D are where *Leucanthemum vulgare* and *Centaurea nigra* ground-truth data were gathered. 'Grass Train' and 'Grass Acc' plots are where training and accuracy assessment pixels respectively were gathered for the 'other' category. 'Achillea Train & Acc' and 'Chamerion Train & Acc' are where training and accuracy assessment pixels were gathered for *Achillea millefolium* and *Chamerion angustifolium* respectively. (**b)** Ground-truth areas for UAV$_{Set2}$. Plots used for gathering training and accuracy assessment data are labelle for each species respectively and the 'other' classification category. Area$_1$ is highlighted in blue on image (b).

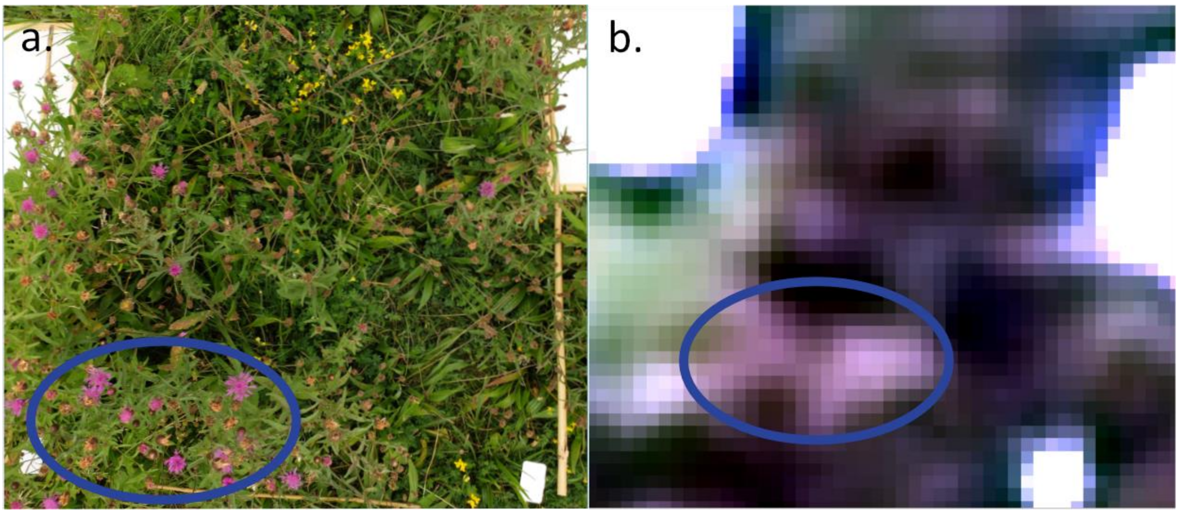


Figure 4.3 a. A $1m^2$ sub-plot marked out on the ground with a patch of *Centaurea nigra* circled. **b.** The same $1m^2$ sub-plot visible within UAV_{Set1} imagery and the same patch of *C. nigra* circled.

For *C. nigra*, two of the four ground-truth plots were selected for training the classifications (Target training plots) and, two were selected for choosing verification pixels (Target verification plots) to be used in an independent accuracy assessment process (see Sections 4.2.5 and 4.2.6). Upon viewing the UAV_{Set1} imagery, it was found that two Target training plots would not allow enough *L. vulgare* verification pixels (64 pixels– see Section 4.2.1) to be gathered for use within the accuracy assessment process. One target training plot was consequently initially used for gathering *L. vulgare* training data and the remaining three plots were used for selecting *L. vulgare* verification pixels (target verification plots).

Locating floral units was dependent upon a floral species having a spectral signature different to any other feature immediately adjacent to it (Dash et al., 2019). Any species with similar colours in the visible (Red-Green-Blue) wavelength range within the $10m^2$ ground-truth plots were subsequently removed. It should be noted that it was impossible to remove tiny floral units (<5mm) such as those belonging to species such as *Vicia hirsuta* or *Epilobium tetragonum* (Stace, 2010). These were so tiny and sparse however, that it was assumed that they would not interfere with the spectral signatures of the target flowering plant species.

Each of the *C. nigra* and *L. vulgare* plots marked out with GCPs were left established for use as ground-truth plots during acquisition of UAV_{Set2} imagery. However, by the 30th

July, the flowering peak of *C. nigra* and *L. vulgare* was over and very few floral units of either species were left in these plots. Subsequently, for UAV_{Set2}, one new plot each for *L. vulgare* and *C. nigra* were marked out respectively using GCP boards (see locations in Figure 4.2b). Each of these was divided into two sub-plots, with one used for gathering training pixel data and the other used for gathering independent verification data. No other flowering plant species of similar colours were present within the plots (although see note above regarding very tiny floral units). It was therefore assumed that within UAV_{Set2} imagery, any patches within the *C. nigra* plot that were the same colour as *C. nigra* (a distinct pink/purple) were indeed floral units of *C. nigra*. Similarly, any patches within the *L. vulgare* plot that were white were assumed to be floral units of *L. vulgare*.

As plots established for UAV_{Set1} were still marked out (see note above) and had a few floral units left, for one of the UAV_{Set2} classification training set iterations (UAV_{Set2} classification iteration 3 – see Section 4.2.6), training data was added from two of these plots originally established for UAV_{Set1}, to see whether data from more than one plot location improved classification accuracies.

4.2.4 Ground-truth data for control sites

For UAV_{Set1} and UAV_{Set2} imagery four 'grass' control plots within $Area_1$ were established, again marked out by GCP boards (See Figure 4.2a and 4.2b). For both sets of imagery, these four control plots contained no *Leucanthemum vulgare* or *Centaurea nigra*. They would therefore serve to demonstrate whether other features such as soil or other non-floral plant matter were being classified as either of the species of interest. They did contain the odd floral unit of species with similar colours to *L. vulgare* or *C. nigra* in the visible range, such as *Silene dioica*. The first two of these grass control plots were located in areas with short grass which had been recently mown. The second two were located in long grass margins. Various other floral species that were not similar in appearance to *L. vulgare* or *C. nigra* were present in the control plots, such as the bright yellow Asteraceae species, *Helminthotheca echioides*.

One long-grass control plot and one short-grass control plot were selected for gathering training data and one of each type of control plot were selected for gathering independent verification data (see Sections 4.2.5 and 4.2.6).

For UAV_{Set1}, *Achillea millefolium* was selected as a control species for *L. vulgare* and was subsequently included as a classification category (see Figure 4.3a and 4.3b). The two species have clusters of small white flowers. A plot containing abundant *Achillea millefolium* was marked out using white GCP boards. This plot was later divided into two sub-plots in QGIS version 3.4 with each sub-plot used respectively to gather *Achillea millefolium* training and independent verification pixels. *Chamerion angustifolium* was used as the control species for *C. nigra*. Although structurally very different, both species produce an abundance of pink/violet floral units. A plot containing abundant *C. angustifolium* was once again marked out using GCP boards and divided into two sub-plots to serve as sections for gathering training and verification data respectively.

For UAV_{Set2}, *Daucus carota* was selected as a control species for *L. vulgare*. *C. angustifolium* and *Epilobium hirsutum*, combined into one 'willowherb' classification category, were selected as control species for C*. nigra*. Two plots in separate fields containing abundant *D. carota* were divided into two sub-plots each (total of four sub-plots). One sub-plot in each plot was used for gathering classification training data and one was sub-plot in each plot was used for gathering independent verification data. For *E. hirsutum* and *C. angustifolium*, two plots (one for each species) located in different areas of the same field were divided into two sub-plots each with one sub-plot used for gathering training data and one for gathering verification data.

Figure 4.4 The flowering plant species each constituting a classification category within the classification maps produced for UAV_{Set1} and UAV_{Set2}. **a.** *Leucanthemum vulgare* and **d.** *Centaurea nigra* are the two target nectar-rich flowering plant species. **b.** *Achillea millefolium* and **c.** *Daucus carota* are the control species for *L. vulgare* in UAV_{Set1} and UAV_{Set2} respectively. **e.** *Chamerion angustifolium* is the control species for *C. nigra* in UAV_{Set1} and UAV_{Set2}. **f.** *Epilobium hirsutum* is combined with *C. angustifolium* into a 'willowherb' control group in UAV_{Set2}.

4.2.5 Training data

For both UAV_{Set1} and UAV_{Set2}, 500 points were randomly selected across the short-grass and long-grass control training plots. These points were used to select 500 'seed' pixels that were used to grow multi-pixel training regions with similar spectral properties, e.g. training regions for green leafy vegetation. As in Chapter 2, all of these training regions were amalgamated into an 'other' classification category that contained features that I was not interested in classifying individually as sub-categories e.g. patches of soil, green vegetation, dry grassy vegetation, shadow and so on. Table 4.2 below outlines the total number of training pixels included in the training set for each of the classification categories, as well as the sub-categories that together formed the 'other' classification category, for UAV_{Set1} and UAV_{Set2} respectively.

Table 4.2 Total number of training pixels in each classification category for each set of UAV imagery

Imagery Set	Classification Category	Number of pixels included in classification training set
UAV_{Set1}	Other	12903
	Achillea millefolium	45
	Chamerion angustifolium	50
	Centaurea nigra	40
	Leucanthemum vulgare	46
	Cirsium	**37**
$UAV_{Set\ 2}$	*Daucus carota* when 2 margins	43
	Centaurea nigra pinkest	50
	Leucanthemum vulgare whitest	49
	Willowherb	48
	Extra 'other' from *Centaurea nigra* and *Leucanthemum vulgare* training plots	23
	Extra 'other'	774
	Other	13502

Note: The table includes the number of pixels included in the training set of the classification iteration that achieved the highest overall classification accuracy for each set of UAV imagery (iteration 4 for UAV_{Set1} and iteration 8 for UAV_{Set2}). *Cirsium* pixels are highlighted in bold as they were not included in UAV_{Set1} classification iteration 4, but were added later to the training set to carry out two classifications by first including *Centaurea nigra* and *Cirsium* as separate classification categories, and then combining them into a single ($Thist_{group}$) classification category.

For each of the flowering plant species classification categories, 50 pixels were selected for inclusion within the training set from the training plots for each species. In order to cover spectral variability, each pixel was selected from a different floral cluster (up to 50 clusters). If there were fewer than 50 clusters, additional pixels were then selected from the same clusters so that there was a total of 50 floral pixels for each flowering plant species (see Figure 4.5 below). Previous research (Chapter 2) identified that the best classification results were obtained when selecting the pinkest or whitest pixels (depending on flower species and based on subjective judgement) from the centre of floral clusters, i.e. those pixels that are less likely to be mixed with other features. Pixels were therefore initially selected from the centre of floral clusters to be used as training data.

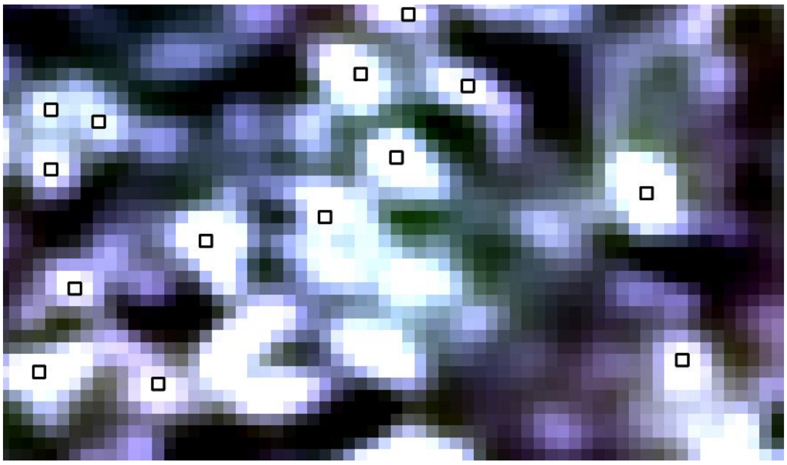


Figure 4.5 Clusters of *Achillea millefolium* clearly visible as large white patches within UAV_{Set1} imagery. *A. millefolium* pixels that were included as training data are outlined in black. One pixel was selected from the centre of each cluster.

4.2.6 Classifications and accuracy assessments

For the initial round of classifications for each set of UAV imagery, maximum likelihood (ML) classification algorithms were applied using the Semi-automatic classification plugin in QGIS version 3.4 (see Chapter 2 for full details of this classification method). Each classification was applied to a sub-section of $Area_1$ to reduce the processing power required. See Appendix 4.2 to see example classifications for the sub-sections of $Area_1$ for both UAV_{Set1} and UAV_{Set2}.

Several iterations of the ML classifier were applied to each set of UAV imagery, having adjusted the training set each time (see Appendix 4.3). For example, extra training regions would be added to the 'other' category if features within the 'other' category were being confused with a particular flowering plant species within the error matrix (see Table 4.2 above). For UAV_{Set1}, training data had initially only been collated from one plot for *Leucanthemum vulgare* (see Section 4.2.3), as three plots were needed to select 64 verification pixels (see UAV_{Set1} classification iterations 1 – 3 in Supplementary Data 6 – accompanying the thesis digitally). However, user's and producer's accuracies for *L. vulgare* were very low in these classification iterations. For classification iteration 4, *Leucanthemum vulgare* training pixels were subsequently added from one of the plots initially used for gathering verification pixels to see whether training data collated from across two plots would improve classification accuracies. The plot could therefore no longer be used for gathering verification pixels, meaning that fewer pixels were included in the error matrix for this iteration (53 as opposed to 64).

For UAV_{Set2}, classification iteration 3 was applied having added additional *Centaurea nigra* and *L. vulgare* training pixels from two plots originally established for UAV_{Set1} (see Section 4.4.3 above).

In addition to the ML classifications carried out in QGIS, a random forest (RF) classifier was applied to UAV_{Set1} and UAV_{Set2} imagery. The RF classifier was applied using the 'RSToolbox' package (Leutner et al., 2019) in R, (R, 2021). The RF classifier was only applied using the training set iterations for UAV_{Set1} and UAV_{Set2} respectively that led to the highest overall accuracies with the ML classifier (UAV_{Set1} iteration 4 and UAV_{Set2} iteration 8, see Supplementary Data 8 and 9 respectively). As different software can lead to variations in classification output, an ML classification was applied to each set of UAV imagery using the 'RSToolbox' package (Leutner et al., 2019) in R rather than QGIS. The ML classifier was only applied using the respective training set iterations for each set of UAV imagery that had led to the highest overall classification accuracies when using the ML classifier in QGIS. The ML classifications carried out in QGIS are hereafter referred to as ML_{QGIS} and the ML classifications carried out in R studio as ML_{RST}.

Classification accuracy assessments were carried out for ML_{QGIS}, ML_{RST} and RF classifications via pixel-based error matrices using the same method as outlined in Chapter 2. The number of verification pixels included in the accuracy assessment for each classification category can be found in Table 4.3 below. For the RF and ML_{RST} classifications and for the ML_{QGIS} classifications that achieved the highest overall accuracies for each set of UAV imagery respectively, an area-based error matrix was calculated following the method of Olofsson et al. (2013). Area-based error matrices account for classification error. Rather than calculating the area allocated to each classification category directly from the classification raster, an area estimator that excludes commission error and incorporates omission error is calculated (Olofsson et al., 2013).

Table 4.3 The number of verification pixels for each classification category for UAV_{Set1} and UAV_{Set2}

UAV Set	Classification category	Number of verification pixels included in accuracy assessment
UAV_{Set1}	Other*	640
	Centaurea nigra	64
	Leucanthemum vulgare	64 (53 for classification iteration 4 and for classifications including *Cirsium*)
	Chamerion angustifolia	64
	Achillea millefolium	64
	Cirsium (Only for classifications containing *Cirsium* [See section 4.2.7])	64
UAV_{Set2}	Other*	640
	Centaurea nigra	64
	Leucanthemum vulgare	64
	Willowherb	64
	Daucus carota	64

*Note that the ‘other’ category is a different set of pixels for each set of UAV imagery

4.2.7 *Cirsium* / *Centaurea nigra* combined classification category

The third research question asked whether *Centaurea nigra* and *Cirsium* thistles around the study site could be accurately classified as individual classification categories, or whether they were best combined into a single classification category. As with previous flowering plant species, 50 pixels of training data from UAV_{Set1} were collated for *Cirsium* species. These consisted mostly of *Cirsium arvense* (see Figure 4.6), although included some pixels of other *Cirisum* species which also share a similar morphology such as *Cirsium vulgare*. A couple of floral units of *Dipsacus fullonum* were present in the plots used to gather *Cirsium* training and verification pixels. However, this was unlikely to appear similar to *Cirsium* species from the air, as the flowers run in two parallel lines around an oval-shaped floral unit which would therefore appear brown from the air.

To the training set for UAV_{Set1} ML_{QGIS} classification iteration 4, the *Cirsium* data was initially added as a *Cirsium* classification category separate to *C. nigra*. The *Achillea millefolium* and *Chamerion angustifolium* classification categories were also amalgamated into the 'other' classification category for simplification. This new training set was used to carry out an ML_{QGIS} classification. *C. nigra* and *Cirsium* training data were then combined into one *Cirsium* / *Centaurea nigra* classification category within the training set. This classification category is hereafter termed $Thist_{group}$. An ML_{QGIS} classification was again applied. Accuracy assessments were carried out using pixel-based and area-based error matrices as with all previous classifications.

Figure 4.6 a. *Cirsium arvense*, the flowering plant species very similar in appearance to **b.** *Centaurea nigra*.

4.2.8 Correlating UAV and ground floral surveys

The fourth research question asked whether the area classified as $Thist_{group}$ (proportion of classified floral cover / m^2) was correlated with the number of floral units of $Thist_{group}$ on the ground (floral units / m^2). To address this question, only UAV_{Set1} imagery was used. An ML_{QGIS} classification was carried out for 15 of the 16 margin sections described in Section 4.2.1. Margin 2 was not used as it had a high tree cover. The margin sections were 105m long X 6m wide. The training set for UAV_{Set1} *Cirsium* classification iteration 2 was used to train the classifier (see Section 4.2.7 above). This training set amalgamated *Cirsium* thistle species and *Centaurea nigra* data into the $Thist_{group}$ classification category.

No new pixel-based error matrices were carried out for individual UAV_{Set1} margin classifications as it was assumed overall, user's and producer's accuracies obtained from pixel-based error matrices would be the same as for the UAV_{Set1} $Area_1$ classification using the same training set.

However, area-based error matrices adjust overall and producer's accuracies according to the area allocated to each classification category as a proportion of the total area of the classification. New area-based error matrices were therefore constructed for each of the 16 margins (see Supplementary Data 10 – digitally accompanying the thesis). The area in each margin section classified as $Thist_{group}$, as derived from each area-based error matrix (m^2), was then divided by the total area of the margin to obtain an estimate of the area classified as $Thist_{group}$ (proportion floral cover / m^2).

Floral surveys were carried out between 1^{st} July and 27^{th} July 2020, to calculate the mean number of $Thist_{group}$ floral units (*Centaurea* / *Cirsium*) per m^2 for each of the 16 margin sections. The number of floral units were calculated in ten $1m^2$ quadrats placed every 10m along a 90m transect in each of the 16 margin sections, following the same method as described in Chapter 3, Section 3.2.3.

A Spearman's rank correlation test was subsequently calculated in R version 4.0.5 (R, 2021) to test for a correlation between the area classified as $Thist_{group}$ (proportion $Thist_{group}$ / m^2) for each margin and, the mean number of floral units / m^2 for each margin. A sensitivity analysis was also carried out. This involved removed some floral units that I had included as *Cirsium vulgare* in the original correlation, but which had been recorded in the raw data using a different code and therefore there was some uncertainty as to whether they were *Cirsium vulgare* or another thistle.

4.3 Results

4.3.1 Overall classification accuracies for maximum likelihood and random forest classifiers

Pixel-based error matrices were created for each UAV_{Set1} and UAV_{Set2} ML_{QGIS} classification iteration (see Supplementary Data 6 and Supplementary Data 7). Overall classification accuracies were calculated for each error matrix. The overall accuracies for the ML_{QGIS} classification iterations that achieved the highest overall accuracies for UAV_{set1} (iteration 4) and UAV_{set2} (iteration 8) respectively, can be found in Table 4.4 below. The ML_{QGIS} classification iterations that achieved the highest overall accuracies for UAV_{Set1} and UAV_{Set2} were then used to train a Random Forest (RF) classifier and an ML classifier in RStudio (ML_{RST}). The pixel-based error matrices for these RF and ML_{RST} classifications can be found in Supplementary Data 8 and Supplementary Data 9 and the overall accuracies are presented in Table 4.4.

For the ML_{QGIS} classifications that achieved the highest overall accuracies for each set of UAV imagery respectively and, for the RF and ML_{RST} classifications, area-based error matrices were constructed. The area-based error matrices can be found in Supplementary Data 8 and 9 and the overall accuracies can be seen in Table 4.4.

For UAV_{Set1}, pixel-based overall accuracies ranged between 87.2% and 91.8%, depending on adjustments made to training sets in each ML_{QGIS} classification iteration. In UAV_{Set1} classification iteration 3, pixels on the edge of clusters of *C. nigra* and *L. vulgare* floral units were added to the training set (see Chapter 3, Section 3.2.5 for a full description of edge pixels). Adding training pixels on the edge of clusters reduced the overall accuracy from 88.5% to 88.2%. In UAV_{Set1} classification iteration 4, *L. vulgare* training pixels were included from across two margins rather than one. This increased the overall accuracy from 88.5% to 91.8%. Classification iteration 4 was subsequently the UAV_{Set1} classification iteration with the highest overall accuracy.

Table 4.4 The highest overall classification accuracies achieved for UAV_{Set1} and UAV_{Set2} classifications

Classification	Overall accuracy for pixel-based error matrices (%)			Overall accuracy for area-based error matrices (%)		
	ML_{QGIS}	**ML_{RST}**	**RF**	**ML_{QGIS}**	**ML_{RST}**	**RF**
UAV_{Set1}	91.75	92.66	43.84	90.73	92.13	64.06
UAV_{Set2}	88.17	82.92	69.98	89.28	87.67	83.81

Note: ML = Maximum Likelihood. ML_{QGIS} are the ML classifications carried out in QGIS and ML_{RST} are the ML classifications carried out in Rstudio. The ML_{QGIS} classifications presented in this table are those classification iterations for each set of UAV imagery that achieved the highest overall accuracies (iteration 4 for UAV_{Set1} and iteration 8 for UAV_{Set2}). RF = Random Forest. The RF classifications were carried out in Rstudio.

For UAV_{Set2}, pixel-based overall accuracies ranged between 31.1% and 88.2% depending on classification iteration. For example, the only difference between UAV_{Set2} classification iteration 2 with an overall accuracy of 77.3% and classification iteration 3 with an overall accuracy of 75.2% was that *Centaurea nigra* and *Leucanthemum vulgare* training pixels in the latter had been collated from two different plots within the image rather than one. UAV_{Set2} classification iterations 7 and 8 had respective overall accuracy values of 82.5% and 88.2%. This difference was due to the fact that classification iteration 8 included *Daucus carota* training pixels from two plots rather than one (see Appendix 4.3).

For UAV_{Set2} ML_{QGIS} classification iteration 7, extra training pixels were added to the 'other' classification category from the plots also used to gather *Leucanthemum vulgare* and *Centaurea nigra* training pixels. This did not make a great difference to the overall accuracy, leading to a 0.11% increase from 82.37% to 82.48%.

For both UAV_{Set1} and UAV_{Set2}, the ML classifications led to higher overall accuracies than the RF classification, when calculated from both pixel-based and area-based error matrices respectively. For UAV_{Set1}, the ML_{RST} classification led to the highest overall accuracy out of the three classifications, calculated from both pixel-based and area-based error matrices (Table 4.4). For UAV_{Set2}, ML_{QGIS} led to a higher classification accuracy than ML_{RST} using both the pixel-based and area-based error matrix approaches.

For the ML_{QGIS} classification iterations that achieved the highest overall accuracy for UAV_{Set1} and UAV_{Set2} and, the RF and ML_{RST} classifications, the area allocated to each classification category can be found in Table 4.5. Table 4.5 also includes the adjusted area for each classification category, calculated using the area-based error matrices, along with the standard error of area estimates.

4.3.2 User's and producer's accuracies for flowering plant species

User's and producer's accuracies were calculated for each of the classifications described in Section 4.3.1 (see Supplementary Data 6-9 for the error matrices). The user's and producer's accuracies for both the UAV_{Set1} ML_{QGIS} classification iteration that resulted in the best overall accuracy and the ML_{RST} and Random Forest (RF) classifications for UAV_{Set1} can be found in Table 4.6. User's and producer's accuracies for the UAV_{Set2} ML_{QGIS} classification iteration with the highest overall accuracy can be found in Table 4.7, as can the user's and producer's accuracies for the RF and ML_{RST} classifications. Accuracies were calculated from pixel-based and area-based error matrices respectively.

The ML_{QGIS} classification iterations with the best user's and producer's accuracies for individual species were not necessarily the classification iterations with the highest overall accuracies. For example, one ML_{QGIS} classification iteration for UAV_{Set2} resulted in a producer's accuracy of 67.2% for *Centaurea nigra* rather than the 25.0% found in Table 4.7. However, user's accuracy was only 14.1% for that particular classification iteration and overall accuracy was only 43.0%.

ML classifications achieved higher user's accuracies than the RF classification for UAV_{Set1}, for all flowering plant species other than *A. millefolium*. Note that user's accuracies are exactly the same whether using an area-based or pixel-based error matrix. For $UAV_{Set2,}$ user's accuracies were higher with the ML classifications than with the RF classification for all flowering plant species other than *D. carota*, for which the RF classification user's accuracy was higher.

When considering the pixel-based error matrices for UAV_{Set1}, the highest producer's accuracies were achieved by an ML classification for all flowering plant species other than *C. nigra*, for which the RF classification achieved the highest producer's accuracy. When

Table 4.5 Area allocated to each classification category in the original classifications for UAV_{Set1} and UAV_{Set2} and following adjustments using an area-based error-matrix

Classification category	Area classified (m^2)			Adjusted area from area-based error matrix (m^2)			Standard error (m^2)		
	ML_{QGIS}	ML_{RST}	RF	ML_{QGIS}	ML_{RST}	RF	ML_{QGIS}	ML_{RST}	RF
Set 1									
Other	3779.23	3677.69	3165.45	3913.04	3908.36	4564.83	35.93	37.57	59.50
Achillea millefolium	853.35	734.50	14.05	525.23	617.90	58.96	41.31	35.09	5.95
Chamaerion angustifolium	85.57	44.78	155.45	79.07	68.30	124.09	8.06	13.67	18.32
Leucanthemum vulgare	65.57	138.65	92.78	333.54	239.75	230.99	40.45	34.25	46.19
Centaurea nigra	467.12	655.22	1823.11	399.97	416.54	271.98	28.27	32.63	35.11
Set 2									
Other	4216.64	4042.25	3785.39	3987.27	4052.58	4051.33	46.69	44.58	42.01
Daucus carota	20.07	65.72	46.40	43.33	68.11	93.19	7.27	5.26	9.71
Leucanthemum vulgare	163.25	118.51	145.26	196.63	121.82	186.16	21.90	11.42	21.95
Centaurea nigra	177.39	345.08	624.08	350.13	338.43	209.32	43.02	43.38	29.61
Willowherb	133.89	139.67	110.11	133.88	130.30	171.24	5.67	6.21	25.26

Note: ML stands for Maximum Likelihood. ML_{QGIS} are the ML classifications carried out in QGIS and ML_{RST} are the ML classifications carried out in Rstudio. The ML_{QGIS} classifications presented in this table are those classification iterations for each set of UAV imagery that achieved the highest overall accuracy (iteration 4 for UAV_{Set1} and iteration 8 for UAV_{Set2}).

RF stands for Random Forest. The RF classifications were carried out in Rstudio.

considering the area-based error matrices for UAV_{Set1}, the highest producer's accuracies were achieved by an ML rather than the RF classification for all flowering plant species. For UAV_{Set2}, the highest producer's accuracies derived from both pixel-based and area-based error matrices were obtained when applying an ML classification rather than an RF classification, for all species other than *C. nigra*, for which the RF classification achieved the highest producer's accuracy.

As can be seen from Tables 4.6 and 4.7, species varied greatly in terms of their user's and producer's accuracies. ML_{QGIS} classification iterations also had a large impact on user's and producer's accuracies in some cases (Supplementary Data 6 and 7) For example, for UAV_{Set1} classification iterations 1-3, *Leucanthemum vulgare* had user's and producer's accuracies of 0.0% respectively, using pixel-based error matrices. When *L. vulgare* training pixels were added from a second plot in UAV_{Set1} classification iteration 4, user's accuracy increased from 0.0% to 95.0% and producer's accuracy from 0.0% to 35.9%.

Adding *L. vulgare* training pixels from a second plot in classification 4 also increased the user's accuracy of *Achillea millefolium*. This was because *L. vulgare* verification pixels that were previously being classified *as A. millefolium* were being correctly classified as *L. vulgare*.

Similarly, when looking at UAV_{Set2} ML_{QGIS} classification iterations, the pixel-based producer's accuracy increased from 1.6% to 84.4% when *Daucus carota* training pixels were selected from across two plots (iteration 8) rather than one (iteration 7). No other changes were made to the training set at the same time. The increase in producer's accuracy for *D. carota* also led to an increase in user's accuracy for *L. vulgare* (from 45.2% to 78.8%), as *D. carota* pixels that were previously being incorrectly classified as *L. vulgare* were subsequently being correctly classified as *D. carota*.

Table 4.6 User's and producer's accuracies for UAV_{Set1} imagery for Maximum Likelihood and Random Forest classifiers

Species	Pixel-based error matrix						Area-based error matrix					
	User's Accuracy (%)			Producer's Accuracy (%)			User's Accuracy (%)			Producer's Accuracy (%)		
	ML_{QGIS}	ML_{RST}	RF	ML_{QGIS}	ML_{RST}	RF	ML_{QGIS}	ML_{RST}	RF	ML_{QGIS}	ML_{RST}	RF
Centaurea nigra	**76.92**	63.16	13.29	78.13	93.75	**95.31**	**76.92**	63.16	13.29	89.84	**99.35**	89.08
Leucanthemum vulgare	**95.00**	77.55	39.68	35.85	**71.70**	47.17	**95.00**	77.55	39.68	18.68	**44.85**	15.94
Chamerion angustifolia	84.00	**90.91**	58.00	**98.44**	93.75	90.63	84.00	**90.91**	58.00	**90.91**	59.61	72.66
Achillea millefolium	61.17	81.43	**84.21**	**98.44**	89.06	50.00	61.17	81.43	**84.21**	**99.38**	96.79	20.07

Note: ML stands for Maximum Likelihood. ML_{QGIS} are the ML classifications carried out in QGIS and ML_{RST} are the ML classifications carried out in Rstudio. The ML_{QGIS} classification presented in this table is the classification iteration that achieved the highest overall accuracy (iteration 4).

RF stands for Random Forest. The RF classifications were carried out in Rstudio.

The classifications that obtained the highest user's and producer's accuracies for each flowering plant species for pixel-based and area-based error matrices respectively, are highlighted in **bold**.

Table 4.7 User's and producer's accuracies for UAV_{Set2} imagery for Maximum Likelihood and Random Forest classifiers

Species	**Pixel-based error matrix**						**Area-based error matrix**					
	User's Accuracy (%)			**Producer's Accuracy (%)**			**User's Accuracy (%)**			**Producer's Accuracy (%)**		
	ML_{QGIS}	**ML_{RST}**	**RF**	**ML_{QGIS}**	**ML_{RST}**	**RF**	**ML_{QGIS}**	**ML_{RST}**	**RF**	**ML_{QGIS}**	**ML_{RST}**	**RF**
Centaurea nigra	**33.33**	22.12	20.69	25.00	39.06	**84.38**	**33.33**	22.12	20.69	16.89	22.56	**61.69**
Leucanthemum vulgare	78.79	**86.76**	78.18	81.25	**92.19**	67.19	78.79	**86.76**	78.18	65.41	**84.41**	61.00
Willowherb	**95.38**	89.86	62.50	**96.88**	**96.88**	62.50	**95.38**	89.86	62.50	95.39	**96.32**	40.19
Daucus carota	94.74	85.07	**95.45**	84.38	**89.06**	65.63	94.74	85.07	**95.45**	43.88	**82.09**	47.53

Note: ML stands for Maximum Likelihood. ML_{QGIS} are the ML classifications carried out in QGIS and ML_{RST} are the ML classifications carried out in Rstudio. The ML_{QGIS} classification presented in this table is the classification iteration that achieved the highest overall accuracy (iteration 8).

RF stands for Random Forest. The RF classifications were carried out in Rstudio.

The classifications that obtained the highest user's and producer's accuracies for each flowering plant species for pixel-based and area-based error matrices respectively, are highlighted in **bold**.

In UAV_{Set2} classifications, *C. nigra* user's accuracy decreased from 22.3% to 19.6% between ML_{QGIS} classification iteration 2 and classification iteration 3. The training set for classification iteration 2 included *C. nigra* training pixels from one plot and the training set for classification iteration 3 included *C. nigra* training pixels from two plots. Producer's accuracy remained the same between the two classification iterations at 42.2%. The user's accuracy for *L. vulgare* decreased from 48.6% to 46.8% and the producer's accuracy decreased from 82.8% to 81.3% between ML_{QGIS} classification iteration 2, which included *L. vulgare* training pixels from one plot, and classification iteration 3, which included *L. vulgare* training pixels from two plots.

4.3.3 Classifying *Centaurea nigra* / *Cirsium* individually and as a combined classification category

The pixel-based and area-based error matrices for the UAV_{Set1} classifications containing *Cirsium* and *Centaurea nigra* as separate and combined ($Thist_{group}$) classification categories respectively can be found in Supplementary Data 11 (digitally accompanying thesis). Overall classification accuracies using each type of error matrix can be found in Table 4.8. Producer's and user's accuracies for each flowering plant species when *Cirsium* and *C. nigra* are classified as individual classification categories can be found in Table 4.9. In comparison, producer's and user's accuracies for each flowering plant species when *Cirsium* and *C. nigra* are classified as a single classification category can be found in Table 4.10.

Table 4.8 Overall classification accuracies for classifications when *Cirsium* / *Centaurea* classified separately and when classified together as a single classification category (Thist$_{group)}$ using a ML$_{QGIS}$ classifier

Classification iteration	Overall Accuracy (%)	
	Pixel-based error matrix	Area-based error matrix
***Cirsium* / *Centaurea* separate**	88.83	62.84
***Cirsium* / *Centaurea* grouped**	91.57	89.34

Table 4.9 User's and producer's accuracies for *Cirsium* / *Centaurea* classification when *Cirsium* species and *Centaurea nigra* are classified as individual classification categories using a ML$_{QGIS}$ classifier

Species	Pixel-based error matrix		Area-based error matrix	
	User's Accuracy (%)	Producer's Accuracy (%)	User's Accuracy (%)	Producer's Accuracy (%)
Leucanthemum vulgare	95.00	35.85	95.00	85.41
Centaurea nigra	56.82	78.13	56.82	99.96
Cirsium spp.	71.88	35.94	71.88	8.53

Table 4.10 User's and producer's accuracies when *Cirisum* species and *Centaurea nigra* are classified as one single classification category (Thist$_{group}$)

Species	Pixel-based error matrix		Area-based error matrix	
	User's Accuracy (%)	Producer's Accuracy (%)	User's Accuracy (%)	Producer's Accuracy (%)
Leucanthemum vulgare	95.00	35.85	95.00	15.18
Thist$_{group}$	82.50	77.34	82.50	92.27

It can be seen from Table 4.9 that when *C. nigra* and *Cirsium* are classified as individual classification categories, that *C. nigra* has a low user's accuracy (56.8%) and *Cirsium* has a very low producer's accuracy (35.9%) when carrying out a pixel-based accuracy assessment. On the other hand, when *C. nigra* and *Cirsium* are combined into one $Thist_{group}$ classification category, user's and producer's accuracies are higher at 82.5% and 77.3% respectively (Table 4.10). Overall classification accuracy is also increased when *C. nigra* and *Cirsium* are combined into one $Thist_{group}$ classification category (Table 4.9).

4.3.4 Correlation between $Thist_{group}$ floral units and area classified

2187 $Thist_{group}$ floral units were counted across 160 quadrats in 16 field margin sections. The mean number of $Thist_{group}$ floral units in each margin ranged between 0 ± 0 (floral units/m^2, 1 S.E., n = 10) and 74.6 ± 13.3 (floral units/m^2, 1 S.E., n = 10) and, can be found in Supplementary Data 12 (digitally accompanying the thesis). An example margin classification can be found in Appendix 4.4 and the area-based error matrices for each margin can be found in Supplementary Data 10 (digitally accompanying thesis).

A Spearman's rank correlation test between mean $Thist_{group}$ floral units (floral units / m^2) on the ground and the area classified as $Thist_{group}$ (proportion of floral cover / m^2) in the UAV_{Set1} margin classifications found a positive correlation of $r_s = 0.61$ ($p = 0.015$). A plot of the area classified as $Thist_{group}$ using UAV_{Set1} imagery and the number of $Thist_{group}$ floral units that this represents on the ground can be found in Figure 4.6. The sensitivity analysis found the same outcome i.e. there was a moderate positive correlation ($r_s = 0.62$, $p = 0.013$) between the $Thist_{group}$ floral units on the ground and area classified as $Thist_{group}$ in the classifications.

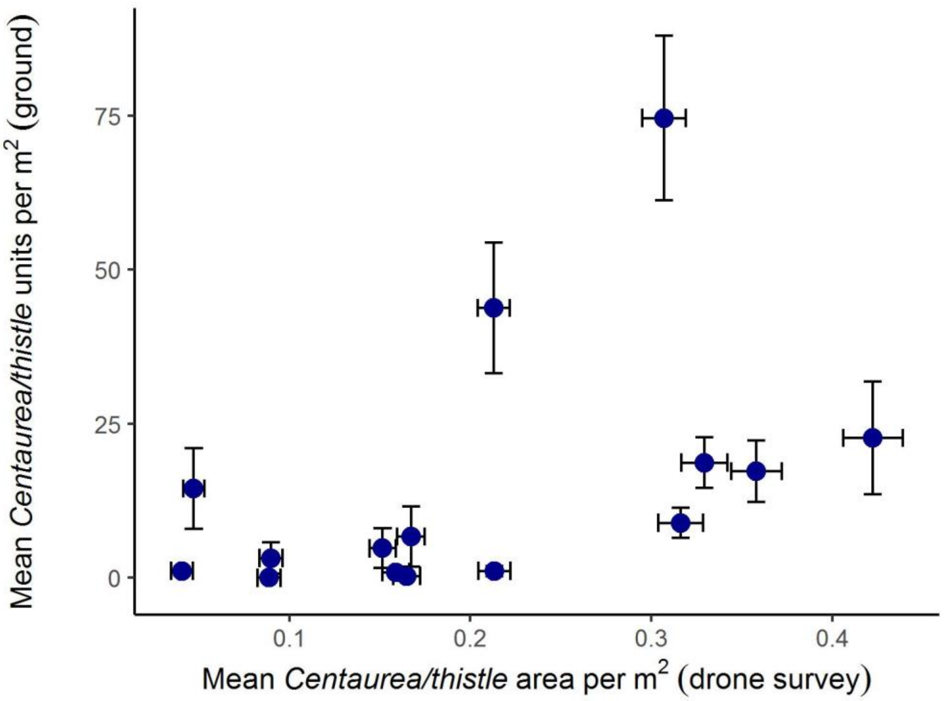


Figure 4.7 Plot of the mean number of *Centaurea*/*Cirsium* floral units on the ground in relation to the area classified as *Centaurea*/*Cirsium* in UAV_{Set1} margin classifications. Each point represents one of 15 margins (Margin 2 was not used in the correlation). Error bars represent standard error. A moderate correlation (r_s=0.61) was found between the two variables (p=0.015).

4.4 Discussion

The first research question for this Chapter asked whether 3cm resolution unmanned aerial vehicle (UAV) imagery can be used to accurately classify the floral component of *Leucanthemum vulgare* and *Centaurea nigra* separately from control species of similar colours. Pixel-based user's and producer's accuracies of 76.9% and 78.1% respectively, were obtained for *Centaurea nigra* in the UAV_{Set1} ML_{QGIS} classification. Accuracies were also high for the control species for *C. nigra*, *Chamerion angustifolia* (84.0% user's accuracy and 98.4% pixel-based producer's accuracy), indicating that the two species are spectrally separable. On the other hand, pixel-based user's and producer's accuracies for *C. nigra* were extremely poor for the UAV_{Set2} ML_{QGIS} classification (33.3% and 25.0% respectively). However, accuracies remained high for the combined willowherb control group which included both *C. angustifolia* and *Epilobium hirsutum* (user's and producer's accuracies of 95.4% and 96.9% respectively), suggesting that it is not confusion with willowherb pixels leading to the low *C. nigra* classification accuracy for UAV_{Set2}. I discuss why *C. nigra* appears to be spectrally separable from its control species in Section 4.4.1 below, as well as a potential reason why low *C. nigra* accuracies were obtained for UAV_{Set2}.

Following the opposite pattern to *C. nigra*, *Leucanthemum vulgare* had a pixel-based producer's accuracy of 35.9% for the UAV_{Set1} ML_{QGIS} classification and 81.3% for the UAV_{Set2} ML_{QGIS} classification. User's accuracies were higher for UAV_{Set1} (95.0%) than for UAV_{Set2} (78.8%) ML_{QGIS} classifications. These differences in *L. vulgare* user's and producer's accuracies between UAV imagery sets were linked to the use of different control species (*Achillea millefolium* in UAV_{Set1} and *Daucus carota* in UAV_{Set2}). I discuss why *L. vulgare* may be separable from one control species and not the other in Section 4.4.1 below.

The second research question asked whether high classification accuracies could be achieved for both *Leucanthemum vulgare* and *Centaurea nigra* using both maximum likelihood (ML) and random forest (RF) classification approaches. Overall, ML classifiers performed well and the RF classifier performed poorly. In UAV_{Set1} for example, the ML_{QGIS} classification resulted in user's and pixel-based producer's accuracies of 76.9% and 78.1% for *C. nigra* respectively, whereas the RF classification resulted in very unbalanced user's and producer's accuracies of 13.3% and 95.3% respectively. For *Leucanthemum vulgare*, pixel-based producer's accuracies were low for both ML_{QGIS} and RF classifications (35.9% and 47.2% respectively), indicating poor performance for both of these classifiers. The ML_{RST} classification however, had user's and pixel-based producer's accuracies of 77.6% and 71.7% for *L. vulgare* respectively. For *C. nigra* in UAV_{Set2}, all three classifiers performed poorly, likely a result of the inseparability of *C. nigra* with other features in the image as discussed in Section 4.4.1. For *L. vulgare* however, both of the ML classifiers performed well, the ML_{RST} classification for example, achieving user's and pixel-based producer's accuracies of 86.8% and 92.2%. The RF classifier performed reasonably well with user's and pixel-based producer's accuracies of 78.2% and 67.2% respectively. The different outcomes for each of the various classifiers and as a result of using different software programmes (QGIS vs RStudio) are discussed in Section 4.4.2.

This study demonstrated that the floral units of *Centaurea nigra* and *Cirsium* species are too similar in appearance to one another to be accurately classified as individual categories using UAV multispectral imagery. This outcome addresses the third research question, which asks whether classification accuracies are improved when combining *Cirsium arvense* and *Centaurea nigra* into one combined $\text{Thist}_{\text{group}}$ classification category rather than when classifying them individually. User's and producer's accuracies were greatly improved when *C. nigra* and *C. arvense* were grouped together into a $\text{Thist}_{\text{group}}$ classification category. A user's accuracy of 82.5% was achieved for $\text{Thist}_{\text{group}}$ rather than 56.8% for *C. nigra* and 71.9% for *Cirsium* when classified individually and, a pixel-based producer's accuracy of 77.3% was achieved for $\text{Thist}_{\text{group}}$, rather than 78.1% and 35.9%for *C. nigra* and *Cirsium* respectively, when classified individually. In Section 4.4.3, I discuss the circumstances under which grouping flowering plant species into a single classification group makes sense from a pollinator perspective, for example if groupings are based on functional traits of relevance to pollinators. I also discuss alternative options, should flowering plant species providing very different functional traits from a pollinator perspective remain spectrally inseparable.

The fourth research question for this Chapter asked whether there was a correlation between the area (proportion of floral cover / m^2) classified as $\text{Thist}_{\text{group}}$ and the number of $\text{Thist}_{\text{group}}$ floral units on the ground (floral units / m^2). A moderate correlation was found between the two variables, indicating that the area classified as *Cirsium*/*Centaurea* could be translated into a relative abundance of floral units on the ground. If the number of floral units on the ground for a particular species are known, the nectar sugar supply provided by that species can also be estimated using data available in the literature (Baude et al., 2015a; Baude et al., 2015b; Table 4.1). Potential reasons for why I did not find a stronger correlation between the two variables are discussed in Section 4.4.4.

4.4.1 Varying classification accuracy outcomes for flowering plant species

User's and producer's accuracies were high for both *Centaurea nigra* and for its control species (*Chamerion angustifolia*) in the UAV_{Set1} ML_{QGIS} classification. The spectral separability of these two species is potentially a result of their having very different floral unit structures. *C. angustifolia* floral units consist of singular pink flowers, while *C. nigra* floral units consist of dense capitula of many tiny disc florets. These differences in morphology could potentially be influencing the spectral signature, despite the superficially similar colour of their petals.

Looking in detail at the error matrix (see UAV_{Set2} classification iteration 8 in Supplementary Data 7) reveals that the low user's and producer's accuracies for *C. nigra* for the UAV_{Set2} ML_{QGIS} classification, are due to the majority of *C. nigra* pixels being classified as the 'other' classification category. Most of the 'other' classification category pixels that were classified as *C. nigra* appear from the image to be dry vegetation/patches of soil (see Figure 4.8). The lower user's and producer's accuracies for *C. nigra* for UAV_{Set2} when compared to UAV_{Set1} could potentially be linked to the fact that by late July more grass/leafy vegetation had dried out and was interfering with the *C. nigra* spectral signature.

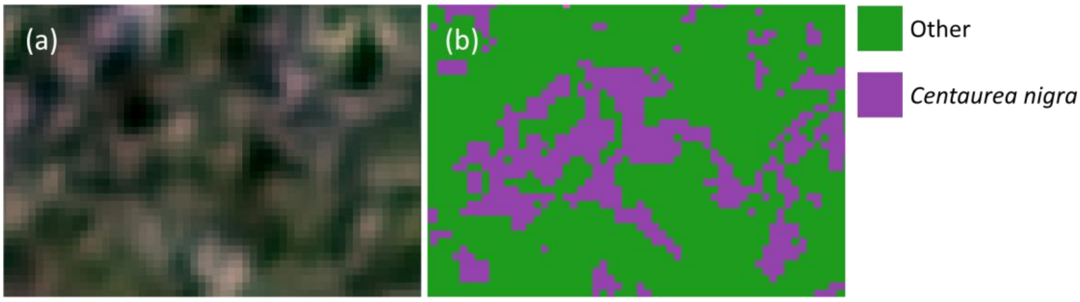


Figure 4.8 (a) A section of UAV_{Set2} imagery showing part of a control plot with no *Centaurea nigra* present and **(b)** grey/brown vegetation being classified as *C. nigra* in UAV_{Set2} ML_{QGIS} classification iteration 8.

In the UAV_{Set1} ML_{QGIS} classification, the majority of *L. vulgare* pixels were classified as *Achillea millefolium*, the control species for *L. vulgare*. This outcome indicates that these two species were not spectrally separable and explains the low producer's accuracy for *L. vulgare* (35.9%). On the other hand, *L. vulgare* was spectrally separable from its control species, *Daucus carota*, within UAV_{Set2} imagery as demonstrated by higher user's and producer's accuracies of User's accuracy *for D. carota* was 94.7% and producer's accuracy was 84.4% within the UAV_{Set2} ML_{QGIS} classification iteration that achieved the highest overall accuracy.

Although *L. vulgare* and *D. carota* are both white flowering species, *D. carota* tends to form looser umbels of flowers through which green leafy vegetation is visible. It is also only the ray florets of *L. vulgare* that are white, while the central disc florets have yellow corollas. These distinctions between the species could explain how they are spectrally separable within high resolution multispectral imagery. Like *L. vulgare*, *A. millefolium* belongs to the Asteraceae family. Both species share a similar floral morphology, having capitula with both ray and disc florets (Andersson, 2008; Sulborska and Weryszko-Chmielewska, 2006). The disc florets in the centre of *Achillea millefolium* are cream in colour and the yellow stamens are often visible. The similar morphologies and colours between the two species could perhaps explain why they are not spectrally separable (see Figure 4.8).

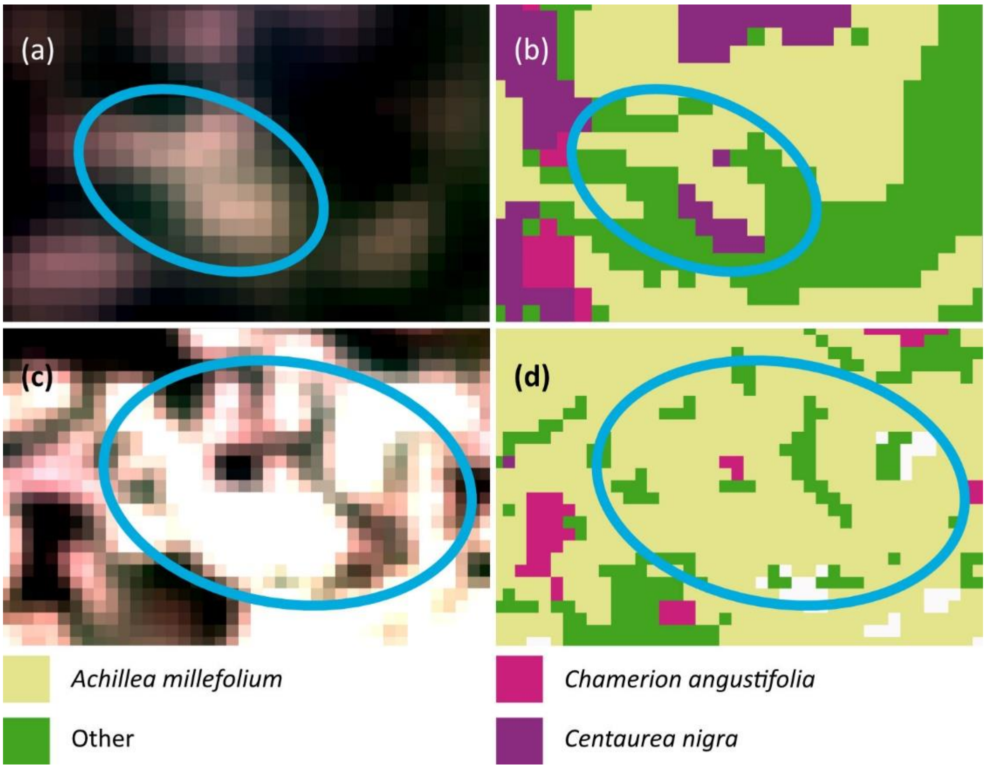


Figure 4.9 (a) A section of UAV_{Set1} imagery showing a patch of *Leucanthemum vulgare* (circled in blue) and **(b)** the QGIS maximum likelihood classification (ML_{QGIS}) of the same section showing *Leucanthemum vulgare* incorrectly classified as *Achillea millefolium* (circled in blue). **(c)** A section of imagery showing a patch of *Achillea millefolium* (circled in blue) and **(d)** the same patch of *A. millefolium* mostly correctly classified, with a few pixels also classified as *L. vulgare*.

4.4.2 Comparing classifiers and classification software

Studies have suggested that machine-learning classification approaches, including Random Forest (RF), lead to higher classification accuracies than maximum likelihood (ML) classifiers (e.g. see Feng et al., 2015; Nitze et al., 2012). The results of this study demonstrate that this is not necessarily the case. UAV_{Set1} ML_{QGIS} and ML_{RST} classifications achieved higher overall accuracies than the RF classification for both pixel-based (91.8%, 92.7% and 43.8% respectively) and area-based (90.7%, 92.1% and 64.1% respectively) accuracy assessments. Similarly, the RF classification for UAV_{Set2} imagery had a lower overall accuracy than both ML classifications when considering pixel-based accuracy assessments (overall accuracies of 70.0% for RF, 88.2% for ML_{QGIS} and 82.9% for ML_{RST}) and area-based accuracy assessments (overall accuracies of 83.8% for RF, 89.3% for ML_{QGIS} and 87.7% for ML_{RST}) respectively.

The results of this study subsequently corroborate the results of Xie et al. (2019), who found that their ML classifier performed better when classifying a variety of forest and non-forest land-cover types than RF and various other machine-learning based classifiers, when they used solely spectral data. For example, when amalgamating data from two different seasons but only incorporating spectral data into the classification, a ML classifier achieved a 76.4% overall accuracy as opposed to the 69.8% overall accuracy of a RF classifier under the same conditions. In my own previous research on mapping nectar-rich flowering plant species (see Chapter 2), an ML classifier also resulted in high overall accuracies when classifying 3cm resolution imagery. Overall accuracies ranged from 92.3% to 98.7%, depending on the month.

On the other hand, Xie et al. (2019) also found that machine-learning based classifiers performed better than ML when additional data such as textural features were incorporated, with the best overall classification accuracy of 84.5% achieved by a support vector machine classifier. A suggestion for future research therefore, is that more traditional parametric classification approaches such as ML not be automatically excluded, but instead be considered alongside machine-learning approaches. This is an important consideration given the rapidly expanding availability of studies using machine-learning approaches (Belgiu and Drăguţ, 2016) and their increasing availability via GIS platforms (Congedo, 2021).

The results of this study also demonstrate that the same classification method applied using different software does not necessarily lead to exactly the same classification outcome (see Tables 4.6 and 4.7 and Figures 4.9 and 4.10). ML classifications were applied to both sets of UAV imagery, first using the Semi-automatic classification plugin (Congedo, 2021) in QGIS (QGIS, 2020) and second using the 'RSToolbox' package (Leutner et al., 2019) in R (R, 2021). For both pixel and area-based accuracy assessments, the ML_{RST} classification achieved the higher overall accuracy for UAV_{Set1} (see Table 4.4). The opposite was true for UAV_{Set2}, whereby the ML_{QGIS} classification resulted in the higher overall accuracy for both pixel-based and area-based accuracy assessments (see Table 4.4).

Differences in classification outcome were likely due to differences in how the ML classifications were applied. The 'RSToolbox' package randomly selects a fixed number of points within polygons of each classification category that are then used to train the classification algorithm (Leutner et al., 2019). On the other hand, the SCP plugin uses all of the collated training data pixels within the classification algorithm (Congedo, 2016). Whether one approach leads to higher classification accuracies for a particular flowering plants species than the other, could potentially depend on the spectral variability in the dataset for that species. Where spectral variability is very high in a dataset for example, having a smaller quantity of training data (as in the case of ML_{RST}) may reduce some of the spectral noise (relative to using the whole dataset through the ML_{QGIS} classifier). On the other hand, if the ML_{RST} classifier randomly selects training points that are not very representative of the spectral signature of a particular flowering plant species as a whole, the accuracy of the ML_{RST} classifier may be lower relative to the accuracy of the ML_{QGIS} classifier. In future research it could therefore be worth trialling different software packages even when using the same overarching classification approach, as in this study, to find the most accurate option for individual flowering plant species.

4.4.3 Spectrally inseparable flowering plant species

In the introduction (Section 4.1.3) I noted that *Cirsium* thistles and *Centaurea nigra* could potentially be classified more accurately as a single classification category, as they share a similar colour, similar flower density within floral units and similar floral unit morphologies. This study demonstrated that these two species were more accurately classified as a combined $\text{Thist}_{\text{group}}$ classification category. However, if flowering plant species are going to be grouped together into a single classification category, the implications in terms of mapping the nectar sugar resource available to pollinators need to be considered.

The different morphological, biochemical or reward features that can vary between flower species and influence flower-visitors are termed functional traits (Fornoff et al., 2016). The floral resource offered by a flowering plant species is a function of both the floral reward quantity/quality traits, as well as the morphological traits that are influencing floral reward accessibility for a particular pollinator individual. Focusing on the nectar reward, flowering plant species vary substantially as to their nectar sugar production (μg/flower/day; Baude et al., 2015). A greater nectar sugar supply has been demonstrated to be beneficial to pollinators, for example by increasing bumblebee colony density (Timberlake et al., 2021) and butterfly species richness and abundance (Holl et al., 1995). When considering a range of plant traits, Fornoff et al. (2016) found that a higher nectar sugar concentration also led to a higher frequency of pollinator visits.

A further requirement for flowering species to be grouped into a single classification category, in addition to sharing physical traits that make them spectrally indistinguishable from one another, could be that species must also share similar nectar sugar supply values (mg/floral unit/day). In the case of *Cirsium* species and *C. nigra*, these are all relatively high values, for example 10705.7 mg/floral unit/day for *C. nigra* and 6539.7 mg/floral unit/day for *Cirsium arvense*, when compared to other species present at the study farm such as *Leucanthemum vulgare* (2137.5 mg/floral units/day) or *Achillea millefollium* (42.3 mg/floral unit/day). However, *C. arvense* still only produces 61% of the nectar sugar supply produced by *C. nigra*, which means that grouping the two species together and calculating their mean nectar sugar supply, would introduce a large quantity of error if using the area classified as a combined *C. arvense*/*C. nigra* category for estimating the nectar sugar supply across a farmed landscape. Combining these two species, or any others, into a single classification category would therefore require assumptions regarding the relative proportion of each species within a habitat. Chapter 3 demonstrates for example, that in sown wildflower margins at the study farm, *Centaurea nigra* is far more abundant than *Cirsium arvense* or any other *Cirsium* species. Identifying the relative proportions of these species within different habitat types commonly found in UK agricultural landscapes would be a useful focus for future research.

Separately to the nectar sugar supply of a particular flowering plant species, it has been shown that as both nectar tube width (mm) decreases and nectar tube length (mm) increases, the number of flower-visiting species decreases (Stang et al. 2006). This is likely because visitors with long proboscides can visit nectar tubes of varying depths, while those with shorter proboscides are restricted to shorter nectar tubes (Klumpers et al., 2019). Foraging efficiency is also affected by nectar tube morphology, with Klumpers et al. (2019) finding that progressively shorter Hymenopteran proboscides, relative to the length of Asteraceae nectar tubes, lead to a greater length of time required to handle an individual flower and a slower extraction rate for nectar sugar. Fornoff et al. (2016) also demonstrate the influence that floral morphology can have upon pollinator visitation frequency, as a greater floral morphology functional diversity led to a reduced frequency of pollinator visits. In terms of nectar accessibility therefore, a further consideration is that flowering plant species could be grouped into a single classification category based on the accessibility of their nectar sugar to different pollinator species, in addition to their overall nectar sugar supply.

However, if spectrally inseparable flowering plant species provide a very different nectar sugar supply, or have very different morphological traits that limit the nectar sugar access to certain pollinator taxa, it may not be sensible to classify them as a single category. Alternative options need to be considered in this instance. In Chapter 3, I demonstrated that 91% of the nectar sugar supply (mg/m^2/day) of sown wildflower margins at the study farm was produced by *Centaurea nigra*. Only 7% of the nectar sugar supply was produced by *Leucanthemum vulgare* in the same margin type and 0.01% was produced by *Achillea millefolium*. In situations such as this, where the nectar sugar supply is dominated by one or a few species, if the aim of a remote sensing survey is to map the nectar supply available to pollinators, spectrally inseparable flowering plant species that only provide a small proportion of the nectar sugar supply could potentially be removed from the survey. In other field margins and at different farms however, floral composition and density is likely to differ and the nectar sugar supply may be contributed more evenly by a greater number of flowering plant species. In this instance, trialling different classification approaches may be more appropriate for determining whether flowering plant species that are spectrally similar when using multispectral data can still be classified separately.

In Chapter 2, I discussed the use of hyperspectral data. Near-continuous spectral data obtained via hyperspectral sensors, as opposed to a few wide bands of data obtained via multispectral sensors (Ustin et al., 2004), may allow subtle spectral differences to be found even between similarly coloured flowering plant species. Green leafy vegetation belonging to different plant species can have very different spectral signatures when using hyperspectral data, linked for example to different biochemical properties and structural features (Asner et al., 2008; Ustin et al., 2004). It has also been shown that the different flowering stages of *Centaurea solstitialis*, from bud to post flowering, have distinct spectral signatures due to changing levels of pigments and water content (Ge et al., 2006). It is possible therefore that hyperspectral data could also pick up on biochemical and structural differences between flower species. However, a significant disadvantage of hyperspectral data acquisition is the considerable cost involved (de Sá et al., 2018) and the relative costs and benefits of hyperspectral versus multispectral data would need to be considered on a case-by-case basis.

Another option could be to employ an object-based classification approach. Unlike a pixel-based approach as I have used in this study, object-based classification looks at the wider contextual detail within which pixels are placed, such as shapes created by clusters of similar pixels (Müllerová et al., 2017). Pixels are then classified based on where they lie within this contextual framework rather than being classified individually based on their spectral information alone (e.g. Burnett and Blaschke, 2003; Müllerová et al., 2017; Vannier and Hubert-Moy, 2008). Müllerová et al. (2017) found this a useful strategy for classifying *Heracleum mantegazzianum* which has a very distinct shape. Other species found at the farm used in this study, such as *Heracleum sphondylium* (see Chapter 3), may therefore benefit from this approach. However, whether species that do not form shapes very distinct from one another, such as *A. millefolium* with corymbose capitula clusters and *L. vulgare* with individual capitula, can be separated using an object-based approach would need further investigation.

4.4.4 Limitations – correlation between Thist$_{group}$ floral units and area classified

A moderate correlation was found between the area classified as Thist$_{group}$ (proportion of Thist$_{group}$ / m^2) and the number of floral units (mean floral units / m^2) on the ground. This is similar to a study by de Sá et al. (2018) which looked at the correlation between *Acacia longifolia* flowers / m^2 and the proportion of *A. longifolia* flower cover / m^2. Weak correlations were found at a couple of sites where *A. longifolia* was in its peak flowering period ($r^2 = 0.128$, $p < 0.01$; $r^2 = 0.156$, $p < 0.01$ respectively), whereas non-significant correlations were found at sites where *A. longifolia* was past the flowering peak (de Sá et al., 2018). The weak correlation in this study and that by de Sá et al. (2018) demonstrate the complexity of trying to match floral units on the ground to the area classified. De Sá et al. (2018) note the habitat variability of their study site, as well as the variable structure of *A. longifolia* plants, as being potential reasons for the low correlation between floral units and area classified.

The correlation between Thist$_{group}$ floral units and area classified in this study could have been weakened for similar reasons. For example, the 16 margins at the study farm consisted of two different margin types (naturally regenerated and sown with a wildflower mix) with differing species compositions (see Chapter 3). Some plant species have features which may have been erroneously classified as Thist$_{group}$ floral units. Chapter 2 demonstrated for example, classification errors between *Silene vulgaris* with pink floral units and woody branches. This study demonstrated that dry grassy patches in Area$_1$ control plots were sometimes classified as *Centaurea nigra*. Woody plant species or patches of dry grassy vegetation present in each of the 16 margins could have potentially led to similar classification errors with Thist$_{group}$ floral units. Soil type also varied across the margins (see Appendix 4.5). Any floral / environmental variability such as this increases the potential spectral variability between margins, which could reduce the strength of correlation between the $Thist_{group}$ floral units / m^2 on the ground and the area (proportion of floral unit cover / m^2) classified as $Thist_{group}$.

One limitation of this study therefore, is the fact that training and accuracy assessment plots were not included in each individual margin, but only in $Area_1$. There could be spectral variation between margins or between $Area_1$ and the margins, linked to the factors described above such as, the presence/absence of woody plant species, flowering plant species not accounted for in $Area_1$ or, soil type. Carrying out an accuracy assessment in each individual margin would have accounted for any of this potential spectral variability.

A second limitation of this study is that the correlation between $Thist_{group}$ floral unit counts and the area classified as $Thist_{group}$ was made at the margin level, i.e. the mean $Thist_{group}$ floral unit count/m^2 was compared to the mean $Thist_{group}$ floral cover /m^2 for each margin. De Sá et al. (2018) marked out different quadrats within their study sites and directly correlated the number of floral units of *A. longifolia* in each quadrat with the floral cover of *A. longifolia* in each quadrat as determined through classified imagery. This provides a more direct measure of correlation. Quadrat surveys only ever cover a small proportion of the habitat/site being surveyed and, in this study, may not have been picking up variation in floral density. This could be one reason for not having a strong correlation between the floral unit counts and area classified and is an issue that would be resolved by having a direct measure of correlation (floral units in each quadrat directly compared to classified floral cover in each quadrat) as used by De Sá et al. (2018). A direct measure of correlation would also potentially allow the environmental features that are weakening the correlation between floral units and classified area to be identified. For example, soil type or the cover of woody plant species could be included in a linear model alongside the number of $Thist_{group}$ floral units, to determine which variables are contributing to the area classified as $Thist_{group}$ within a given margin.

4.4.5 Conclusions

This study has demonstrated that nectar-rich floral resources can be mapped using 3cm resolution multispectral UAV imagery with high overall accuracies. User's and producer's accuracies varied considerably with date of image acquisition for *Leucenthemum vulgare* and *Centaurea nigra*. Some variability in accuracies could be linked to environmental variables such as weather conditions. For example, a greater quantity of dry vegetation later in the summer after a period of hot weather could be a potential reason for lower *C. nigra* accuracies in late July. This raises the question as to whether the variability in classification accuracies are trends that repeat on a yearly basis and within different agricultural landscapes. For *L. vulgare*, changes in accuracies were linked to the use of different co-flowering control species in UAV_{Set1} (*Achillea millefolium*) and UAV_{Set2} (*Daucus carota*). Different farm locations would also have different co-flowering species compositions alongside focal nectar-rich flowering plant species. A next step would be to scale-up this research and assess the classification accuracies of the nectar-rich flowering plant species considered here across multiple years and farming locations. I discuss this further in Chapter 5.

Nonetheless, while recognising the current limitations, high-resolution UAV data shows great potential as a means of extending current crop monitoring within arable fields (Daponte et al., 2019; Norasma et al., 2019) into the adjacent field margins. This would thereby provide a means of assessing the foraging resources already available to pollinators. Targeted decisions could then be made as to the subsequent field margin management for the benefit of pollinators and biodiversity more widely.

Chapter 5

Progressing the Research and Applications for Pollinator Conservation

At the start of this PhD thesis I set out with two overarching aims. Firstly, I wanted to determine whether fine-scale within-habitat nectar resources available to pollinators could eventually be captured using remote-sensing technology. Secondly, I wanted to investigate how the variation in the within-habitat nectar resource affects pollinator abundance. In this final Chapter, I discuss how my findings have met these aims and contributed to the wider body of knowledge on pollinator conservation and ecology. I then discuss the shortcomings of the research, as well as future opportunities.

Chapter 2 started to address the first PhD aim by asking whether remotely-sensed multispectral imagery of 3cm and 7cm resolutions could be used to accurately classify five key nectar-rich flowering plant species within arable field margins and hedgerows. These two habitat types have the potential to provide key foraging resources for pollinators within arable farming systems, which are frequently resource-poor (Baude et al., 2016; Timberlake et al., 2019; Häussler et al., 2017). Imagery was acquired via a manned aircraft platform. Both imagery with 3cm and 7cm spatial resolutions achieved high overall classification accuracies (ranging between 92.3% and 98.7%), although for *Crataegus monogyna* and *Silene dioica* with low 7cm imagery producer's accuracies (54.7% and 52.0% respectively), 3cm producer's accuracies were marginally better (65.6% and 64.1% respectively). While 7cm data generally performs well on these five species, use of the higher resolution data could subsequently be more appropriate for some key nectar-rich species.

In Chapter 4, I determined the accuracy with which unmanned aerial vehicle (UAV) multispectral imagery could classify two of the highest nectar-sugar-producing flowering plant species at the study farm, when co-flowering control species with similarly coloured floral units were included in the classification. Imagery acquired had a 3cm spatial resolution. Overall accuracies were also high, ranging between 88.2% and 91.8%, while once again user's and producer's accuracies were variable.

Direct comparisons could not be made between the remote-sensing platform types. This was due to a number of differences between them in the data acquired, such as radiometric resolution and the number of data layers included in the final multispectral composite images (UAV imagery had a red-edge layer which manned aircraft imagery did not). Although marginally better overall accuracies were achieved with manned aircraft data, good overall accuracies were achieved with both platforms; above the 80-85% minimum accuracy suggested in the remote sensing literature (e.g. see Foody, 2008 and Xavier et al. 2018). When carrying out pixel-based accuracy assessments on maximum likelihood classifications for 3cm imagery, the overall accuracies obtained with manned aircraft data ranged between 92.3% and 98.7%, whereas for UAV data they ranged from 88.2% to 91.8%. User's accuracies for individual flowering plant species were more variable, ranging from 77.8%-98.3% for classifications using manned aircraft data and 33.3-95.4% for UAV data. Producer's accuracies were similarly variable ranging between 64.1%-95.3% and 25.0-96.9% for classifications using manned aircraft and UAV data respectively. Choice of remote sensing platform is also likely to vary depending on the operational advantages and disadvantages of each platform type as I discuss in Section 5.3.

A second research question in Chapter 4 asked whether species that are very similar in appearance can be classified more accurately together as a single functional group, rather than individually. *Cirsium arvense* and *Centaurea nigra*, two co-flowering, nectar-rich species with floral units of similar colours and morphology were used as a case study for this question. Combining *Cirsium arvense* and *Centaurea nigra* into a single functional group (Thist$_{group}$) increased the overall pixel-based classification accuracy by 2.7%. The user's accuracy of Thist$_{group}$ (82.5%) was higher than both the user's accuracies for *C. nigra* (56.8%) and *C. arvense* (71.9%). The producer's accuracy for Thist$_{group}$ (77.3%) was also higher than the producer's accuracy for *C. arvense* (35.9%), although slightly lower than the producer's accuracy for *C. nigra* (78.1%). These accuracies highlight the benefit of combining *C. nigra* and *C. arvense* into a single classification category. However, as I discuss in Chapter 4, from a pollinator conservation perspective it is only useful to group flowering plant species together when they share spectral characteristics, if they also share functional traits important to pollinators, such as levels of nectar and pollen resource, or accessibility of those resources to different taxa. In Section 5.1, I discuss potential alternative options for separating flowering plant species using remoting sensing, in circumstances where spectrally inseparable species are functionally different from a flower-feeding insect perspective, continuing the discussion from Chapter 4.

The user's and producer's accuracies obtained for different flowering plant species classification categories in Chapters 2 and 4 provide useful information as to how well individual pixels are allocated to the correct classification category. However, the number of pixels classified as the floral component of a particular flowering plants species does not automatically inform us as to the number of floral units that this represents on the ground. Without knowing the number of floral units represented on the ground, we cannot calculate the nectar sugar supply (mg/floral unit/day). In order to calculate this last missing piece of information, in Chapter 4 I tested whether there was a correlation between the area classified as $Thist_{group}$ (proportion of floral cover / m^2) and the number of $Thist_{group}$ floral units on the ground. There was a moderate correlation between the two variables ($r_s = 0.61$; p=0.015). Reasons for the lack of a stronger correlation between the variables were discussed in Chapter 4, such as the fact that the correlation was carried out by calculating the mean number of floral units (floral units / m^2) at the margin level, based on a relatively small sample, rather than by directly correlating the count of floral units within each quadrat with the area classified as $Thist_{group}$ (proportion floral cover / m^2) within each quadrat, as other authors have done (e.g. De Sá et al., 2018).

The correlation between area classified and the number of floral units on the ground has only been assessed for one classification category in this PhD project. Similarly, the user's and producer's accuracies using different remote-sensing platforms and classifiers has only been assessed for a small number of the entomophilous flowering plant species potentially encountered within an arable landscape (Baude et al., 2016). It would take considerable time and effort to determine whether all of these species can be mapped using remote-sensing technology and whether they can spectrally be separated from one another. Additionally, it is likely that many of the species that do share similar colours and morphological features would not be separable from one another (as with *Leucanthemum vulgare* and *Achillea millefolium* in Chapter 4). If remote-sensing technologies are to be employed for estimating the nectar-sugar availability within arable field margins and hedgerows in the future, decisions therefore need to be made about which entomophilous flowering plant species to include in this process. I consider the potential directions in Section 5.2.

The research presented throughout this thesis was carried out at one study farm in one UK-based location. Even once decisions have been made as to which flowering plant species should be included in a remote sensing programme for estimating nectar-sugar availability, the methods must be repeated across multiple farm locations with varying environmental conditions. The potential variables that should be considered within future research are discussed in Section 5.4. However, once the accuracy with which key nectar-rich flowering plant species / functional groups can be classified using high-resolution remote sensing technology is known, the potential applications for managing farm-level pollinator habitat or modelling pollinator community metrics are far-reaching. These are discussed in Sections 5.5 and 5.6.

Studies have calculated differences in the nectar-sugar supply between broad habitat types (Langlois et al., 2020; Timberlake et al., 2021) or managed landscapes (Langlois et al. 2020) and linked this to pollinator metrics such as colony density (Timberlake et al., 2021) or abundance (Langlois, 2020). Others have identified farm (Timberlake et al., 2019) and landscape-level (Jachuła et al., 2021) nectar-sugar gaps according to honeybee and bumblebee nectar sugar demand estimates throughout the year. Hicks et al. (2016) looked at the nectar-sugar supply ($mg/m^2/day$) of different commercially-available sown wildflower mixes but did not link this to any pollinator metrics. The second thesis aim has not been extensively addressed within the pollinator literature (although see Holl et al., 1995). This is most likely a result of the time- and labour-consuming nature of mapping the cover or abundance of individual flower species.

To address my second thesis aim, in Chapter 3 I asked whether there was any correlation between the total nectar sugar provision ($mg/m^2/day$) of arable field margins and the margin-level bee abundance. Honeybee abundance, was found to positively correlate with the margin level nectar sugar provision. Two margins were particularly influential in driving this relationship and were highlighted as outliers in the bee abundance model by a

Cook's Distance test. I subsequently discussed honeybee recruitment strategies, which were likely leading to the very high honeybee abundance in these two influential margins.

When the two margins were removed from the model, only margin type (naturally regenerated or sown with a wildflower mix) was found to have an effect upon honeybee abundance. The sown wildflower mix margins had a significantly greater number of honeybees than the naturally regenerated margins. Similarly, when considering wild bees (bumblebees and solitary bees), only margin type was found to have a significant effect upon wild bee abundance. This was potentially still linked to nectar sugar quantity, as the sown wildflower margins had a significantly higher nectar sugar production overall than the naturally regenerated margins. However, as discussed in Chapter3, semi-natural habitat was a confounding variable which also differed with margin type and as such, it was not possible to disentangle the effects of these two variables. Other variables could have also been influencing bee abundance between the two margin types such as the local availability of nesting resources and pollen.

The primary focus of this PhD project has been nectar sugar as the key pollinator energy source (Willmer et al., 2011). However, in terms of meeting the spatial and temporal foraging requirements of pollinators, a number of gaps remain that have not been addressed in this PhD project. In Chapter 3, I used bee abundance as the dependent variable, when studying the effect of nectar sugar supply across arable field margins. However, there are many other pollinator metrics that could be used to measure availability of nectar/pollen. I consider some of these in Section 5.7. Pollen was not considered in this thesis and yet, it is an integral component of the pollinator diet, as it provides the main protein source, along with other macronutrients (Vaudo et al., 2016; Weiner et al., 2010). I discuss this further in Section 5.8. Different pollinator species also have varying life-histories and functional traits that influence both their nutritional and floral resource accessibility requirements. I consider how these differences must be incorporated in future bee abundance models in Section 5.9.

5.1 Addressing overlapping spectral signatures between flowering plant species

In both Chapter 2 and Chapter 4, nectar-rich flowering plant species that were spectrally inseparable from one another were encountered. Various options can be considered for addressing this issue.

In Chapter 2, *Crataegus monogyna* pixels were confused with *Anthriscus sylvestris* when applying a maximum likelihood classification algorithm to manned aircraft data. In future studies, this situation would not be complicated to resolve. In this particular instance, *C. monogyna* was located in the hedgerow and *A. sylvestris* in field margins. Each feature (hedgerow and field margins) could be classified individually while masking the other feature, thereby solving the issue of the two species not being completely spectrally separable. Alternatively, a vegetation height layer could be incorporated into the classification, which would immediately separate the hedgerow from the margin.

In other situations, for example where two spectrally inseparable species are both present in field margins, flowering plant species could be grouped together according to functional traits that make them spectrally similar from a remote sensing point of view and, similar in terms of the traits such as nectar sugar content, flower height and morphology that have been shown to influence pollinator visits (Fornoff et al., 2016). I demonstrated in Chapter 4 that this could be done with *Centaurea nigra* and *Cirsium arvense*, both of which are tall flowering species with a high nectar sugar supply (Baude et al., 2016) and which are both purple and with morphologically similar flowers.

On the other hand, the situation is more complex when two flowering plant species that are not functionally similar are also not spectrally separable. This was the case with *Leucanthemum vulgare* and *Achillea millefollium* in the study focusing on UAV data (Chapter 4). These species both have relatively tall, white, showy floral units with cream / yellow centres. However, they vary considerably in their nectar production with *A. millefolium* producing 42 µg/floral unit/day compared to the 2138 µg/floral unit/day produced by *L. vulgare* (data from Baude et al. (2015a) and Baude et al. (2015b)). From a practical sense, a decision could be made in this instance as to whether a remote sensing survey or traditional transect and quadrat survey is carried out. A quick scan of a sub-set of field margins at a farm may indicate that only one of the two species is present, therefore meaning that a remote sensing survey could be employed for estimating the distribution and abundance of that species. If both species are present in great abundance, a traditional transect/quadrat survey may be more viable.

If a remote sensing survey is still the preferred option, for example because it provides data on the large-scale spatial distribution of a species rather than the estimated mean abundance within a particular area (Henrys and Jarvis, 2019), other remote sensing classification approaches could be trialled. Hyperspectral data for example, gathers near-continuous spectral data across the wavelength range under consideration, which could draw out differences in spectral signatures between plant species that would not be found using multispectral data (Kattenborn et al., 2019). However, the high cost of hyperspectral data may not be justifiable relative to the increase in accuracy obtained (Bradter et al., 2020; Huang et al., 2010).

Object-oriented methods have been employed for various applications, for example to classify woody hedgerow habitat (Vannier and Hubert-Moy, 2008) or different vegetation species (Laliberte et al., 2011). Instead of relying on the classification of each pixel individually, object-based image analysis involves segmenting pixels into distinct portions that are subsequently classified using a range of metrics from shape to spectral properties (Burnett and Blaschke, 2003; Vannier and Hubert-Moy, 2008; Tansey et al., 2009). Laliberte et al. (2011) note for example, that object-based image analyses can be very useful for high-resolution data because they can overcome some of the issues surrounding in-class spectral variability. It is possible therefore, that even if species such as *A. millefolium* and *L. vulgare* are not spectrally separable, that other properties such as textural features (Tansey et al., 2009) or floral unit clustering patterns could allow them to be distinguished via an object-oriented method.

If, despite considering all other remote sensing options, certain flowering plant species remain spectrally inseparable, there could still be value in using high-resolution, remotely-sensed data to rapidly visualise the relative diversity of flowering plant species of different colours that are present within a margin. This suggestion is underpinned by the theory of pollination syndromes, which proposes that different flowering plant species have evolved specific traits, such as flower colours and shapes, through convergent coevolution, to target different pollinator species groups (Fenster et al., 2004; Trunschke et al., 2021). Studies have found preferences for certain flower colours by different groups of pollinators, although these innate preferences can also be overridden by learnt associations between flower colours and reward availability (e.g. see Goyret et al., 2008; Trunschke et al., 2021).

Reverté et al. (2016) found that pollinator groups had preferences for certain flower colours, with purple for example, being the colour of choice for bees. However, different flower colour groups were not linked to distinct pollinator community compositions, with one suggestion for this result being generalisation of the pollinator community (Reverté et al., 2016; Waser et al., 1996). The study also indicates that the pollination syndromes theory may work from the pollinator perspective but not from the plant perspective (Reverté et al., 2016). Hoyle et al. (2018) found significant effects of flower colour diversity on the abundance of hoverflies and bumblebees. However, the direction and significance of effects depended on the method used to estimate abundance and time of year of the surveys (Hoyle et al., 2018). For example, a higher hoverfly abundance was found in plots with a high flower colour diversity as opposed to a low flower colour diversity when using sweep net surveys carried out in August. The opposite relationship, i.e. lower hoverfly abundance in high flower colour diversity plots, was found when carrying out visual counts of hoverflies visiting floral resources across three surveys from June-September (Hoyle et al., 2018).

While the relationship between flower colour and particular pollinator groups has not been definitively clarified, at the simplest level, a greater floral abundance and species richness can increase the abundance and richness of pollinators (Haaland and Bersier, 2011; Wix et al., 2019). Fornoff et al. (2017) found that increasing the diversity of flowers with different reflectance values, increased pollinator visitation frequency. Trunschke et al. (2021) noted that no studies have specifically looked at the interactions between flower colour and resources such as nectar. This would be an interesting area for future research, particularly if the diversity of floral colours mapped using remote-sensing technology can be linked to a basic estimate of nectar-sugar supply. Alternatively, it is possible that a few species are driving the nectar supply across margins or within hedgerows. This was the case at the study farm in this PhD project (*Centaurea nigra* was the species producing 81.1% of the nectar sugar supply across 16 margins – see Chapter 3). If these species can be classified with a high classification accuracy, a basic estimate of the spatial distribution of the farm-level nectar sugar supply could also be obtained.

The extent and diversity of floral resources of different colours as mapped using remote-sensing technology could therefore be developed as a simplified way of assessing overall floral abundance and species richness and identifying gaps across agricultural landscapes at large scale (for example a whole farm or a section of a farm, such as $Area_1$ in this study which was ~0.34 km^2 in size – see Chapter 4). Xavier et al. (2018) found for example, a positive relationship between floral cover within 0.25m^2 plots as estimated from UAV imagery and the number of pollinators. They did not break down floral cover into individual species or colour categories which could subsequently also be a useful piece of future research.

Mapping floral resources according to broad colour categories may be of little value in agricultural landscapes with an already abundant and species rich flora. However, many agricultural landscapes are very simplified and with scarce floral resources. It is also in these landscapes that agri-environment interventions have been shown to have the greatest positive effect upon pollinators (e.g. Scheper et al., 2013; Wix et al., 2019). Mapping the flowering plant species diversity across simplified agricultural landscapes, according to the diversity of floral colours, could locate the areas in which additional agri-environmental measures or management practices would have the greatest effect.

The continued provision of an abundant and species-rich flora in field margins over a number of years is important for the maintenance of a rich and abundant pollinator community, yet many field margins reduce in floral abundance and richness over time (e.g. Carvell et al., 2007; Pywell et al., 2011; Wix et al., 2019). Others increase, for example as perennial species establish (Carvell et al., 2007). The remote sensing of floral resources of different colours could potentially allow these changes to be monitored over time and indicate, for example, when a grass and wildflower margin needs to be re-established.

5.2 Which nectar-rich flowering plant species should be targeted within future remote-sensing programmes?

The accuracy with which 10 flowering plant species can be classified using high-resolution remotely-sensed data has been calculated through this PhD project. A further species, *Epilobium hirsutum*, was also classified in combination with *Chamerion angustifolium* as a combined willowherb control group in UAV_{Set2} classifications in Chapter 4. However, if the remote-sensing of nectar-rich flowering plant species is to be used regularly as a technique for estimating the spatial and temporal distribution of the nectar sugar supply within agricultural landscapes, the methods developed through this PhD project need to be tested on further flowering-plant species present within agricultural landscapes across the pollinator foraging season. In this section, I discuss potential ways of prioritising the selection of additional flowering plant species.

Baude et al. (2016) use Countryside Survey data (Carey et al., 2008), their own vegetation surveys within plots of different habitat types and, measured nectar sugar quantities (μg/flower/day), to estimate the mean nectar productivity of different habitat types (Baude et al., 2016). They then scale up this data to provide an estimate of the yearly nectar provision across Great Britain, 90% of which is produced by 22 flowering plant species (Baude et al., 2016). This PhD project has already assessed the classification accuracy of five of these 22 species (Baude et al., 2016): *Cirsium arvense*, *Centaurea nigra*, *Rubus fruticosus* agg., *Crataegus monogyna* and *Achillea millefolium. Cirsium pallustre* and *Cirsium vulgare* are also two of the top 22 national nectar producing species (Baude et al., 2016). These species could also be combined into a *Centaurea*/*Cirsium* functional group classification category as I do with *C. nigra* and *C. arvense* in the UAV study in Chapter 4. Furthermore, *Prunus spinosa* was one of the only species flowering in March at the study farm (Chapter 2). Although not one of the 22 species, *P. spinosa* is one of the top 35 species that together produce 95% of the nectar supply (Baude et al., 2016). One priority for future research could be determining the accuracy with which the remaining top 35 nectar-producing flowering plant species in Great Britain can be classified, using high-resolution multispectral imagery.

However, many of the species producing 90-95% of Britain’s nectar supply are unlikely to be found in an intensive agricultural context, for example *Calluna vulgaris* or *Erica cinerea* (Baude et al., 2016). In light of this, it would be useful to determine the top nectar-rich flowering plant species most commonly found within arable landscapes and that are providing the majority of the nectar forage resource available to pollinators. Classification accuracies for those species could subsequently be determined. Various UK-based and European studies have highlighted several species as being key floral resources in sown grass and wildflower margins and in naturally regenerated margins within agricultural landscapes. This study and others (Critchley et al., 2006; Ouvrard et al., 2018) have demonstrated the ready availability of *Centaurea* species in sown grass and wildflower margins and their importance as a foraging resource for pollinators.

This is not surprising as *Centaurea* species are often suggested for inclusion within agri-environment schemes, for example the ‘AB8 – Flower-rich margins and plots’ option (UK Government, 2021a) or ‘AB1 – Nectar flower mix’ option (UK Government, 2021b), both available within the UK’s Countryside Stewardship agri-environment scheme. As a result, *Centaurea* species are also frequently included within commercially-produced grass and wildflower mixes provided by different seed companies, such as the CSS3 Wildflower Meadow mix provided by Boston Seeds (Boston Seeds, 2021), the ‘EM1 – Basic General Purpose Meadow Mixture’ produced by Emorsgate Seeds (Emorsgate Seeds, 2021) or the ‘KWM2bs Basic Pollen and Nectar Mix’ by Kings Crops (Frontier Agriculture Ltd., 2021). When prioritising flowering plant species to map across different farm systems using remote sensing technology, a key set of the most nectar-rich species that are commonly found in commercial wildflower mixes could therefore be a second option.

In naturally regenerated margins, Critchley et al. (2006) found that *Cirsium arvense* was one of the most frequently found species. Other studies have highlighted the value of *Cirsium* thistles as a pollinator foraging resource including in naturally regenerated margins (Carvell et al., 2004; Ouvrard and Jaquemart, 2018; Pywell et al., 2005; Vray et al.,2017). As in the study outlined in Chapter 2, Blaix and Moonen (2020) found *Rubus* species growing abundantly in margins that weren’t mown on a regular basis. Furthermore, when comparing plant species (both grasses and herbaceous flowering plants) between different margin types (sown with grasses, grasses and wildflowers or naturally regenerated), Critchley et al. (2006) found no difference between margin types in terms of unsown perennial herbaceous flowering plant species. These studies all suggest that a second key set of nectar-rich flowering plant species that are not traditionally included within sown wildflower mixes, but that are frequently found within different margin types in agricultural landscapes in the UK, are also a good focus when prioritising the classification and mapping of nectar-rich floral resources.

It would be useful to combine the prioritisation of nectar-rich flowering plant species included in commercially-available sown wildflower mixes and those unsown species commonly found across all margin types (Critchley et al., 2006). In Chapter 3, I also demonstrated that the nectar sugar supply (mg/m^2/day) of the flowering-plant species that contributed the greatest proportion of the nectar sugar supply could be used as a proxy for the total nectar sugar supply within bee abundance models. Proxy species that contribute the greatest proportion of the margin-level nectar sugar supply could therefore be the focus for future remote-sensing programmes. Future research would subsequently need to identify the flowering plant species contributing the greatest proportion of the margin-level nectar sugar supply (mg / floral unit / day) across different field margins across the UK. A dataset produced as part of the Agriland (Baude et al. 2016) database does provide information as to the proportions of different flowering species found in agricultural habitats across the UK but this data is not publically available.

In addition to sown grass and wildflower mixes and unsown perennials present within arable field margins, annual flower mixes are often sown within arable landscapes. Annual mixes also provide valuable resources for pollinators (e.g. see Carreck and Williams, 2002). They contain a different suite of species to sown wildflower and grass margins and naturally regenerated margins, for example *Centaurea cyanus*, *Borago officinalis* or *Phacelia tanacetifolia*. I have not determined the accuracy with which flowering plant species included in annual mixes could be classified, but this could be an interesting area for future research. However, mapping nectar resources within annual mixes may be less of a priority if the aim is to assess the long-term spatial and temporal availability of floral resources within a farmed landscape, as annual mixes tend to be re-cultivated yearly (Carreck and Williams, 2002). Furthermore, perennial mixes have other advantages to annual mixes, such as the fact that they can provide floral resources earlier in the year (Carreck and Williams, 2002; Hicks et al., 2016) greater quantities of nectar and pollen (Hicks et al., 2016) and have greater melliferous potential, a measure based on nectar production, floral density and the length of flowering (Ion et al., 2018). I therefore suggest that annual mixes are not prioritised in any future remote sensing programmes.

5.3 Manned aircraft or UAV: which remote-sensing platform to choose?

The research presented in Chapters 2 and 4 demonstrated that imagery obtained via manned aircraft and unmanned aerial vehicle (UAV) platforms can achieve high overall accuracies when classifying nectar-rich flowering plant species of importance to pollinators in an agricultural landscape. It also demonstrated that variable user's and producer's accuracies can be obtained for individual flowering plant species.

Centaurea nigra was the only species that was classified using imagery from both platform types. Pixel-based user's and producer's accuracies of 91.8% and 87.5% respectively were obtained for *C. nigra* in maximum likelihood classifications carried out using 3cm manned aircraft data (Chapter 3). In Chapter 4, maximum likelihood classifications carried out on UAV_{Set1} data in early July resulted in pixel-based user's and producer's classification accuracies of 76.9% and 78.1% for *C. nigra* respectively, when using pixel-based accuracy assessments. This decreased to 33.3% for user's accuracy and 25.0% for producer's accuracy for UAV_{Set2}, the reasons for this lower accuracy were discussed in Chapter 4.

The higher user's and producer's accuracies for *C. nigra* when using manned aircraft data compared to UAV_{Set1} data, could be due to differences in training and verification data. No entomophilous flowering plant control species were included as a classification category for classifications carried out using manned aircraft data in Chapter 2. Non-*C. nigra* classification category verification and training pixels were subsequently either selected from non-margin areas (such as the hedgerow) or from areas in the margin that were definitely not *C. nigra* (white flowering plant species for example). The user's and producer's accuracy assessments for *C. nigra* in manned aircraft classifications were therefore potentially overestimated relative to the UAV_{Set1} classification, in which

Chamerion angustifolium, with a similar human-perceived floral colour to *Centaurea nigra*, was included as a classification category control species.

However, the differences in classification accuracy could also be due to the remote sensing platforms themselves. UAV data take a long time to acquire compared to a manned aircraft flight (observations from research presented in this thesis), which can lead to greater variation in light and atmospheric conditions over the course of imagery acquisition (Feng et al., 2015). This is another potential mechanism contributing to the lower user's and producer's accuracies obtained for *C. nigra* via UAV rather than manned aircraft data.

The importance of gathering training data from across the whole image in order to capture variability at a landscape-scale has been highlighted (Horning et al., 2016). However, this could be even more important given the potentially greater variation in environmental conditions as UAV data are acquired (Feng et al., 2015). The classification results derived using UAV data in Chapter 4 highlight the importance of training data acquisition from across different areas of the UAV image. User's and producer's accuracies increased considerably for UAV_{Set1} when *Leucanthemum vulgare* training pixels were included from two plots at separate locations rather than one plot at a singular location. When data for *Daucus carota* was incorporated into the UAV_{Set2} training set from two plots rather than one, producer's accuracy also increased by 82.8%.

Future research empirically investigating the differences in classification accuracy between remote-sensing platforms would be useful for clarifying which platform gives the best classification result when mapping nectar-rich flowering plant species. In order to do this, any other sources of variability, such as radiometric resolution, would need to be kept constant between the two datasets.

In light of the high overall accuracies obtained with both manned aircraft and UAV data (above 85%; see Foody, 2008), the choice of remote sensing platform should perhaps be decided on a case-by-case basis, taking into consideration the operational pros and cons of each platform type (Delavarpour et al., 2021; Feng et al., 2015; Hruska et al., 2012; Landmann et al., 2018). Compared to airborne data obtained from manned aircraft, unmanned aerial vehicle (UAV) data can be more cost-efficient and manoeuvrable and less labour intensive than manned aircraft data (Delavarpour et al., 2021; Feng et al., 2015; Landmann et al., 2018; Xiang et al., 2019). Furthermore, UAV studies do not necessarily require such extensive scheduling (Hruska et al., 2012), for example around take-off/landing.

On the other hand, there are challenges to surmount when acquiring UAV images. In the research presented in this thesis, UAV imagery took a greater length of time to acquire than manned aircraft imagery. The stability of the UAV platform can also be an issue (Feng et al., 2015; Jakob et al., 2017), as can the fact that very high resolution UAV data can pick up on fine-scale topographic changes which can complicate geometric processing (Jakob et al. 2017). Using manned aircraft as opposed to UAV imagery could also be a better solution when covering large study areas (Delavarpour et al., 2021).

5.4 Scaling-up the remote sensing of resources across multiple farms and environmental conditions

I have shown that manned aircraft and unmanned aerial vehicle (UAV) are both suitable platforms for obtaining data to then classify and map nectar-rich flowering plant species (Chapters 2 and 4). However, this PhD research was based at one farm location within the UK. If the methods developed through this research are to be used by conservation or agricultural practitioners on the ground, their repeatability in different farming systems is a key area for future research.

In Section 5.2, I discussed how to prioritise the selection of key nectar-rich flowering plant species to map within typical UK-based agricultural landscapes. However, despite keeping target flowering plant species consistent between farm locations, the spectral signature of the remaining non-target vegetation between survey locations could vary (Gebhardt et al., 2006). This could subsequently influence the accuracy with which the target flowering plant species are classified. The vegetation composition of margins can vary depending on management (Pywell et al., 2011) and/or the successful establishment and continuity of plant species (Cresswell et al., 2019). Establishment and continuity of flowering plant species is linked to many different factors such as compatibility of the soil variables in which the species is grown, or competition from other plants (Cresswell et al., 2019).

Some species for example, will grow well in soils with a high water content, e.g. *Ranunculus* species, while others will not (Critchley et al., 2006).

Critchley et al. (2006) found that field margin plant composition varied with UK geographical region, separately from soil or semi-natural habitat variables. They theorise that one factor that could lead to differences between geographical region could be farm management practices (Critchley et al., 2006). The theory that management practices substantially affect plant species composition is supported by Blaix and Moonen (2020), who found a significant effect upon margin plant composition of adjacent land-use (i.e. cropped, grazed or adjacent to a road), linked to the corresponding differences in margin management practices based on the adjacent land use. Kleijn and Snoeijing (1997) demonstrated that herbicide/fertilizer drift could influence the plant species richness of field margins, with drift also being linked to management practices in adjacent cropped fields. Margin age can also have an effect upon plant composition with Critchley et al. (2006) finding in sown grass margins established after 2001, that as margin age increased, the number of annual herbaceous flowering plant species decreased. The same pattern was not observed for sown grass margins established before 2002 (Critchley et al., 2006).

As well as influencing the success of establishment of different flowering plant species (Cresswell et al., 2019), soil properties could directly influence the user's and producer's accuracies of flowering plant species classification categories. Landmann et al. (2015) found for example, that some pixels of their white acacia classification category, the dominant species of which was *Acacia tortilis*, were confused with soil in the accuracy assessment. This might not be an issue in areas with very dense vegetation where soil/bare ground is not visible, but could be an issue in margins where vegetation is patchy. Soil texture (proportion of clay, loam and sand) is one property that can influence the soil spectral signature (Gholizadeh et al., 2018) and it is possible that the spectral signatures of some texture types overlap with the spectral signatures of individual flowering plant species to a greater extent than others. However, despite a variety of soil types represented by 15 margins included in the study in Chapter 4 (see Appendix 4.5), I still found a positive significant relationship ($r_s = 0.61$; p=0.015) between the area classified (proportion floral cover / m^2) as a combined *Centaurea nigra*/*Cirsium* classification category ($Thist_{group}$) and the mean number of $Thist_{group}$ floral units on the ground (floral units / m^2). This could be an indication that soil texture is unlikely to interfere with the classification accuracy of *Centaurea nigra* / *Cirsium* species within agricultural field margin, although this needs to be confirmed across different farms.

I recommend focusing on soil texture as a starting point for determining the influence of soil properties upon classification accuracy. Other features of the soil such as soil moisture or organic matter, can also influence the soil spectral signature (Gedminas and Martin, 2019; Gholizadeh et al., 2018; Streck et al., 2003; Uno et al., 2005). However, soil moisture can itself be influenced by soil texture, depending on the varying water-holding capacities of different textures (Ahlmer et al., 2018). On the other hand, surveying under consistent weather conditions is important, as completely dry soil has a very different spectral signature to wet soil (Streck et al., 2003). Organic matter constitutes a very small proportion of the dry matter content of the soil. In a study by Gholizadeh et al. (2018) for example, mean proportion of soil organic carbon varied between 1.03% and 1.44% depending on site location. Furthermore, the same study found that the soil organic carbon content also varied to an extent with soil texture anyway (Gholizadeh et al., 2018). However, Goidts and van Wesemael (2007) found that management and use of agricultural land was more important in determining soil organic carbon than texture, indicating that classification accuracy consistency for key flowering plant species should also be tested across margins under different management.

The next step for the research developed in Chapters 2 and 4, is to determine whether nectar-rich flowering plant species can be classified with similar accuracies across different farms. To summarise the discussion above, I suggest that in this scaling-up process, classification training and accuracy assessment plots are included across margins of different ages and experiencing different management practices, to account for potential variability in plant species compositions (Critchley et al., 2006; Pywell et al., 2011) and soil organic matter content (Goidts and van Wesemael, 2007). Varying management practices may be obtained by including study farms from a number of different UK regions as suggested by Critchley et al. (2006). I also suggest including study margins across a range of soil textures and carrying out comparative remote sensing surveys under similar environmental conditions.

In Chapter 4, which focused on the classification of two sets of UAV imagery, time of year had a distinct impact on the user's and producer's accuracies of target nectar-rich flowering plant species. *Centaurea nigra* for example, was classified with a far lower accuracy in UAV_{Set2} at the end of July than UAV_{Set1} at the start of July. I theorised in Chapter 4 that this could be linked to a period of hot dry weather having led to a greater quantity of dry vegetation. Dry vegetation pixels were confused with *C. nigra* in the accuracy assessment process. Leafy vegetation under drought conditions contains less chlorophyll than green healthy vegetation (Vanajith et al., 2021). This leads to greater reflectance in the red wavelength region of the electromagnetic spectrum and the subsequent reddish appearance of dry vegetation (Vanajith et al., 2021) which overlapped with *C. nigra*.

Weather conditions vary considerably on a year-by-year basis. However, an important aspect of scaling up research across multiple farms, could be to determine whether there is an optimal time of year that results in the most accurate classification results for a particular flowering plant species. Alternatively, combining remotely sensed data from different time points throughout the year can lead to increased classification accuracies (Senf et al., 2015). This could be worth investigating if classification algorithms confuse certain flowering plant species with non-vegetative features, as was the case in with *C. nigra* and dry vegetation pixels in the late July dataset in Chapter 4. The dry vegetation was likely still green in early July, meaning that if imagery was combined from the two time points it would be unlikely that a classification algorithm would confuse the vegetation pixels with *C. nigra* floral unit pixels.

In Chapter 2, I studied the accuracy with which known floral unit clusters of the hedgerow species *Prunus spinosa*, *Crataegus monogyna* and *Rubus fruticosus* could be classified and mapped. At the study farm, each species was flowering abundantly and in high densities. However, cutting frequency can hugely influence floral abundance (Staley et al., 2012). Time of year at which hedgerows are cut can also affect floral abundance, with Staley et al. (2012) demonstrating that *Crataegus monogyna* hedges cut in the autumn rather than in the winter have more flowers (% flower cover/0.25m^2 quadrat). In light of this, scaling up the research to include farms with different hedgerow management would determine whether different densities/abundances of hedgerow floral resources could be classified with similar classification accuracies to those obtained in Chapter 2.

5.5 Applications for pollinator management within agro-ecosystems

Should the methods for mapping nectar-rich flowering plant species prove transferable to different farmed landscapes with variable management and soil types, they would be a useful tool for determining the baseline nectar resource available to pollinators. As discussed in previous chapters, many farms already use remote sensing technology either as part of a precision farming policy, or simply for crop monitoring (Daponte et al., 2019; Norasma et al., 2019; Tenkorang and Lowenberg-DoBoer, 2008). One possibility would be to extend crop monitoring practices into the field boundary features, such as field margins and hedgerows, in order to gain an understanding of the nectar resource available to pollinators. Where temporal or spatial gaps in resources are identified, decisions can then be made as to the most appropriate pollinator interventions. Increasing the availability of nectar resources in some areas may be as simple as changing hedgerow management. This is demonstrated by Staley et al. (2012) who found that cutting *Crataegus monogyna* hedges every three years as opposed to every year, led to a 2.1 times greater number of flowers.

In other areas, it may be possible to remove unproductive land (for example field edges) out of cultivation and use these areas to instead create nectar-rich habitat for pollinators (Pywell et al., 2015). These decisions could be aided through the use of decision support tools (DSTs). Rose et al. (2016) found that at least 395 DSTs are already available to farmers and their advisors within the UK. DSTs have been developed to aid appropriate management decisions based on a range of evidence from different sources (Zhai et al., 2020). One such tool is 'Omnia', a precision-farming tool available through H L Hutchinsons Ltd, the iCASE partner to this PhD studentship (Hutchinsons, 2021b). Omnia allows targeted agricultural management through the incorporation of different farm data layers into an individually tailored management plan (Hutchinsons, 2021b).

Examples of data layers include soil variables, weed pressure or yield estimates (Hutchinsons, 2021b). Nectar resources available to pollinators could potentially be incorporated as a data layer within Omnia and combined with other data layers such as overall field performance, which is itself derived from multiple yield estimate (tonnes / ha) maps (Hutchinsons, 2021b). This would allow the selection of those management options that best support both the pollinator community and crop productivity in an intensively-farmed arable landscape. For example, field locations with a consistently poor performance could be removed from production and instead sown with a pollinator-friendly wildflower mix. The resulting potential increase in ecosystem services as a result of increasing semi-natural habitat could provide further yield benefits. This is demonstrated by Pywell et al. (2015), whereby 8% of land was switched from crop production to wildlife habitat without compromising overall crop yield (Pywell et al., 2015).

If spatial data on the availability of nectar resources is to be acquired as a part of routine crop monitoring or for incorporation into DSTs, one future option would be to create a spectral library for nectar-rich pollinator foraging resources that would allow these resources to be identified within remotely-sensed imagery from different farmed locations. Spectral libraries have been created to collate data on the spectral signatures of many different features including soil variables and plants (Baldridge et al., 2009; Kokaly et al., 2017; Shepherd and Walsh, 2002), which can later aid classification within remotely sensed imagery (Schmid et al., 2004). Measurements can be made via a range of platforms including via hand-held spectrometers in the field, in the laboratory or through the use of airborne spectrometers such as AVIRIS, the Airborne Visible / Infrared Imaging Spectrometer (Kokaly et al., 2017; NASA, 2021). However, a spectral library would only be useful if it can be demonstrated that the spectral signatures of different flowering plant species at one farm, are transferable to another farm with a different landscape and environmental context and, that classification accuracies remain consistent between locations (see Section 5.4 above).

Furthermore, in this study I decided not to convert the digital number values to reflectance, the former being the values in each pixel derived from the radiance at each pixel location as measured from the sensor and, the latter having had atmospheric corrections applied (Lillesand et al., 2015). This is because I was not comparing data between different time points (Xavier et al., 2018). If the aim was to create a spectral library and collate data on the spectral signatures of different nectar-rich flowering plant species, digital number values would need to be converted to reflectance so that they would be directly comparable across time and space (Minařík et al., 2019). This could be done using one of the many available techniques, such as empirical line calibration (Smith and Milton, 1999) or radiative transport models (e.g. see Berk et al., 1998).

5.6 Spatial and temporal availability of pollinator resources

The ability to accurately map a core set of nectar-producing flowering plant species in naturally regenerated margins, sown grass and wildflower mixes and hedgerows, would be a step closer to estimating the nectar-resource at the whole-farm level. As discussed in previous chapters, classification layers detailing the floral cover of key nectar-rich flowering plant species could also be included in spatially-explicit models for estimating pollinator/pollination metrics, such as density, abundance or flower-visits (e.g. Gardner et al., 2020; Häussler et al., 2017; Lonsdorf et al., 2009). These models currently use estimates rather than a direct measure of the floral resources available within broad land cover categories. Estimates are either calculated empirically through vegetation surveys that are then extrapolated to the whole-habitat level or, through expert judgement of the floral resources available in different habitat types relative to one another. A direct measure of floral resources as can be achieved using high-resolution remotely-sensed data subsequently has the potential to transform the fit of spatially-explicit models to pollinator data.

Alternatively, spatially-explicit classifications of nectar-rich flowering plant species at different times of year would allow agri-environment interventions to be better targeted towards filling spatial and temporal resource gaps. Management could focus on making sure that nectar resources are well distributed within an agricultural landscape so that they are available to a range of species with differing foraging distances (Nowakowski and Pywell, 2016). As bee body size decreases for example, foraging distances decrease and, some small solitary bees will only travel distances of a few hundred metres from their nests to forage (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007). Zurbuchen et al. (2010) found considerable variability in foraging distance even among individuals of the same species and foraging distances greater than expected when based on body size alone. For example, females of *Hylaeus punctulatissimus* foraged up to 1100m away from the nest. However, 75% individuals foraged no more than 380-400m away from the nest (Zurbuchen et al., 2010), indicating that nectar resources distributed every several hundred metres would still be necessary to ensure the viability of some bee species.

5.7 Pollinator metrics for measuring floral resource availability

In Chapter 3 of this thesis, I looked at how bee abundance varied according to nectar sugar supply (mg/m^2/day) in arable field margins. However, there are many other pollinator variables that could also be measured as alternatives in future research, when establishing the link between floral resource availability and pollinator populations.

Garbuzov et al. (2020) for example, explored how eight pollinator variables changed throughout the foraging season, as well as correlations between each variable, to determine whether these could act as indicators of nectar sugar availability in the landscape. The first three variables were measures of flower-visitor pressure per unit rate of nectar sugar secretion of three flowering plant species (*Phacelia tanacetifolia*, *Borago officinalis, Erysimum linifolium*). This was calculated by dividing flower-visitor counts in patches of each flowering plant species (two per plant) by the rate of nectar sugar secretion at the patch-level. The fourth variable included an index determining the preference of insect foragers for artificial feeders supplying different concentrations of sucrose solution. The index was designed so that higher values indicated poor resource availability in the wider landscape, linked to a higher tolerance of less concentrated sucrose solutions. The fifth and sixth variables included counts of honeybee guards and fights between honeybees respectively (normalized according to size of colony), on the landing platforms of five honeybee hives. These variables were calculated on the premise that guarding and fighting behaviour increases, when foraging resources are in short supply. As a seventh variable, a hanging scale was used to measure change in hive weight (adjusted based on colony size and the number of days that weather was suitable for foraging) across the foraging season. Finally, waggle dance behaviour in six different hives as part of a separate study in the same area, was interpreted and used to estimate honeybee foraging distance. The latter can be indicative of availability of floral resources in the wider landscape, as honeybees will selectively forage from the most rewarding patches over very large distances (Beekman and Ratnieks, 2000).

Significant correlations were found between some of these variables and not others, e.g. honeybee guarding behaviour was correlated with foraging distance, changes in hive weight and flower-visitor pressure on the nectar sugar secretion rate from both *P. tanacetifolia* and *B. officinalis*. This led the authors to suggest that seven of the variables (all other than flower-visitor pressure on nectar sugar secretion rate in *E. linifolium*) were likely changing throughout the foraging season depending on the fluctuation in availability of nectar supply and could subsequently be used as proxies for this nectar availability in the wider landscape. Patterns in nectar availability, suggested by looking at the data from all variables other than flower-visitor pressure on *E. linifolium*, are that nectar is likely in good supply relative to foraging needs in spring and early summer, in shorter supply in late summer before increasing again in the early autumn and dropping considerably in later autumn. A key limitation of the study was that fluctuations in the actual landscape-level nectar availability and therefore, the accuracy with which each variable was representing this resource, was not measured (Garbuzov et al., 2020).

Measures of pollinator reproductive success can also be used as alternative metrics for studying floral resources availability. In 2006 and 2007 for example, Elliot (2009) studied the effect of *Delphinium barbeyi* floral unit density in three Rocky mountain (US) wildflower meadows on the colony reproduction of *Bombus appositus*. *D. barbeyi* constitutes an important pollen and nectar source for this bumblebee species (Elliot, 2009). Following establishment, *B. appositus* colonies were equally distributed across each meadow. Some colonies had been laboratory-bred using captive queens, while others had been attracted to nest boxes positioned in the meadows. After the breeding/foraging season, the number of males and, gyne and worker cocoon abundance, were calculated for each colony. The same study (Elliot, 2009) also looked at whether flower visits (percentage open flowers visited in approximately $20m^2$ sections of meadow) by *B. appositus* minute^{-1} differed across each meadow in 2007. The nectar volume produced by *D. barbeyi* flowers in each meadow and at two time periods (before 0800 and after 1600 hours respectively) was also calculated.

As a whole, colony reproduction in each year remained relatively consistent across each of the three meadows. There was no significant difference in the number of gynes between meadows for either year (p = 0.7 for 2006 and p = 0.6 for 2007) or when looking at data from both years ($p = 0.6$). Similarly, there were no significant differences between meadows in terms of workers or males in 2006 ($p = 0.9$ and $p = 0.9$ respectively) or when considering data from both years ($p = 0.6$ and $p = 0.1$, respectively). In 2007, there was a marginal significant difference in colony worker numbers between meadows ($p = 0.06$), with more workers in the meadow with the intermediate *D. barbeyi* floral density. There were also, in 2007, a significantly higher number of males in this same meadow ($p = 0.04$). There was no significant difference in flower visit rate by *B. appositus* between the three meadows ($p = 0.4$). Flower nectar volume did vary according to meadow ($p = 0.02$), with the meadow with the least *D. barbeyi* flowers also having the highest nectar volume value. The depletion of nectar throughout the day was no different between meadows ($p = 0.2$) and this depletion was less than 30%. The author suggests that the relatively consistent colony reproductive metrics between meadows may have arisen due to the fact that *B. appositus* flower visit rate did not vary according to meadow. As flower density increased, forager density increased, which would mean no increase in floral resource availability for colonies in meadows with more flowers. Meadow-level *D. barbeyi* nectar availability was also unlikely to affect reproductive metrics at the colony level, as such a low proportion was depleted from each meadow throughout the course of a day, even in the meadow producing the lowest nectar volume (Elliot, 2009).

Zacepins et al. (2017) noted that the electronic hive scale for measuring hive weight can be a useful tool for assessing nectar flow into a hive and therefore when foraging resources are in short supply in the vicinity of a hive. When connected to a remote server, near-continuous data can be gathered from the hive scales (Zacepins et al., 2017), which can provide real-time insight into foraging resource availability. Meikle et al. (2008) demonstrated this in their study. They established honeybee colonies in four hives and using electronic scales connected to dataloggers, continuously measured the weight of honeybee hives every hour between June 2004 and July 2006. From these measurements, long-term weight changes were calculated as a daily running average. For a given hour in time, this was calculated as the average hive weight across 25 hours, including the hour in question and the 12 hours on either side. Short-term weight changes within the period of a single day were also calculated by subtracting the daily running average data from the raw data at each time point. A sine function was used for modelling the short-term weight changes within a single day and this demonstrated a stronger sine curve pattern (higher amplitude) in July as opposed to August, due to nectar flow being higher in July compared to August (Meikle et al., 2008). The study demonstrated the potential of using short term hive weight changes linked to nectar flow for assessing nectar resource availability between habitats or within habitats.

In another study by Lecocq et al. (2015), Calpaz hive scales were fitted to honeybee hives, (26 in final analysis) distributed across Denmark, that gathered weight data on a two-hourly basis. Once accounting for weight changes linked to management, the remaining weight changes were linked to changes in colony biomass which were assumed to represent foraged pollen/nectar. The proportions of different habitat categories (e.g. agriculture or semi-natural habitat) and artificial surfaces were also calculated in 1km and 3km radii around each hive. When considering 3km radii, hives in urban landscapes, which were defined as any landscape surrounding a hive which was represented by more than 50% urban land cover type, were found to weigh significantly more than hives in landscapes dominated by agricultural land cover types or in mixed landscapes (p = 0.028 and p = 0.017, respectively) (Lecocq et al., 2015). Nectar and pollen resource variability in each of these land cover types was not investigated in the Lecocq et al. (2015) study, but could form the basis of future studies using hive weight measurements to estimate foraging resources in the wider landscape as an alternative to measuring bee abundance.

5.8 Measuring the margin-level pollen supply

Chapter 1 presents the reasoning behind mapping the availability of nectar sugar, as a starting point when focusing on pollinator foraging resources. Nectar sugar is essential for the day to day functioning of pollinators as it constitutes their main source of energy (Willmer et al., 2011). As reasoned by Baude et al. (2016), nectar sugar (µg/flower/day) also constitutes a common unit that is directly comparable across flowering plant species. However, pollen is equally as important a resource, as it meets pollinator lipid and protein, among other, nutrient demands (Vaudo et al., 2016; Weiner et al., 2010).

Incorporating pollen supply in addition to nectar sugar supply in future bee abundance models like those I carried out in Chapter 3, may therefore potentially improve the model fit. Timberlake et al. (2021) for example, found a significant positive relationship between the pollen supply (volume / floral unit) in September of Year 1 and *Bombus terrestris* colony density (colonies / km^2) the following summer. However, adding pollen supply to their models looking at the relationship between nectar sugar supply (g/ km^2/day) and *B. terrestris* colony density did not improve model fit, with the suggested reason being the significant positive correlation between nectar and pollen supply.

A study by Wood et al. (2017) found that 23% and 16% of solitary bee pollen foraging visits in the mid-summer were made to *Centaurea nigra* and *Leucanthemum vulgare* respectively, both of which are also high nectar-producers (Baude et al., 2016). Ouvrard et al. (2018) similarly found *Leucanthemum vulgare* to be one of the main producers of pollen in sown wildflower strips. These two studies, indicate that there may be a limited set of foraging plant species commonly found within arable farm systems and that are providing the majority of the pollen supply. The correlation between pollen and nectar supply identified by Timberlake et al. (2021) indicates that there may be a substantial overlap between the species providing the majority of the nectar supply and the majority of pollen. Extending the remote-sensing methods developed through Chapters 2 and 4 of this PhD to incorporate the flowering plant species that contribute the greatest volume of pollen, may therefore not require much additional work from a remote sensing point of view. A pollen database for the UK does exist (Timberlake et al., 2021), although this is not yet available to the public. Identifying the flowering plant species contributing the greatest pollen supply would consequently be a useful area in which to focus future research.

5.9 Meeting the foraging requirements and preferences of different pollinator species

Different groups of bees and other pollinators have preferences for different flowering plant species (Michelot-Antalik et al., 2021; Nichols et al., 2019). These preferences can be linked to accessibility, with for example, the accessibility of nectar determined by the shape/size of pollinator mouthparts in relation to the depth/width of flower corollas or other tubular nectar-holding structures (Goulnik, et al., 2021; Stang et al., 2006). Alternatively, floral preferences can be linked to the nutritional provision of their resources in relation to the nutritional requirements of pollinators (e.g. see Ghosh et al., 2020; Hanley et al., 2008; Russo et al., 2018; Vaudo et al., 2015; Vaudo et al., 2016; Vaudo et al., 2020).

Bumblebees for example, focus their foraging on more rewarding resources as demonstrated through a study by Cnaani et al. (2006). *Bombus impatiens* foragers preferentially foraged artificial flowers offering a greater nectar sugar concentration (% sucrose) (Cnaani et al., 2006). Vaudo et al. (2016) found a significant positive exponential relationship between the protein:lipid ratio of pollen from different flowering plant species and the mean community-level *Bombus impatiens* pollen-foraging visits (visits/min/cm^2 floral area/100 bees). Ghosh et al. (2020) demonstrated that honeybees preferentially foraged *Trifolium repens* pollen which had a higher protein content than the other pollens available during the study. This is a similar result to a study focusing on bumblebees (Hanley et al., 2008), where a significant positive relationship was found between the mean protein content of pollen resources (%) and proportion of bumblebee visits (proportion of bumblebee visits to all plant species).

Floral preferences linked to both the composition and/or accessibility of floral resources can subsequently translate up to the plant-visitor network level. Nichols et al. (2019) for example, show that the wildflower species obtaining the highest species richness of solitary bee visitors are a different suite of wildflowers to those with the greatest species richness of bumblebee visitors. A few flowering plant species such as *Taraxacum agg.* or *Crepis capillaris* were important foraging resources for both bumblebees and solitary bees (Nichols et al., 2019). Wildflower species such as *Sinapsis arvensis* and *Convolvulus arvensis* had a high species richness and abundance of solitary bee visitors, while *Centaurea scabiosa* and *Geranium pratense* had a high species richness and abundance of bumblebee visitors (Nichols et al., 2019).

Future models of bee abundance, such as those carried out in Chapter 3, should take into account the variability in pollinator nutritional requirements and foraging preferences. Models could include the nectar-sugar supply according to floral morphology as individual explanatory variables. For example, a possible research question linked to the fact that 'open' flowers are accessible to a greater number of pollinators (Klumpers et al., 2019) could be: ‘Does margin-level bee abundance increase, as the nectar sugar supply (mg / m^2/ day) provided by open-flowering plant species increases?’.

5.10 Conclusions

This PhD project has demonstrated the importance of considering the within-habitat nectar sugar supply in pollinator conservation, as it can vary substantially, for example according to margin type. Margins sown with wildflower mixes targeted to pollinators produced a significantly greater quantity of nectar than margins allowed to regenerate naturally at the study farm. The higher nectar sugar supply of sown wildflower margins was also potentially a contributing factor to the higher bee abundance in sown wildflower margins compared to naturally regenerated margins. Even within the same margin type, the nectar sugar supply varied substantially, highlighting the value of being able to directly measure the nectar resource using remote-sensing technology.

I have shown that nectar-rich flowering plant species can be classified and mapped with high overall classification accuracies (above 85%; see Foody et al., 2008) using remotely-sensed imagery of 3cm and 7cm resolutions and obtained via different remote sensing platforms. The current limitations have also been discussed, such as the fact that certain flowering-plant species remain spectrally inseparable. Ways of addressing these limitations have also been considered, including the application of alternative classification techniques and, mapping flowering plant species according to functional group or more broadly, for example by looking at flower colour diversity.

Additional research will help to clarify other remaining questions, such as whether classification accuracies for individual nectar-rich flowering plant species are consistent across farming systems in different geographical locations, with different soil types and management practices (Cresswell et al., 2019; Critchley et al., 2006; Gholizadeh et al., 2018). Chapter 3 demonstrated that those flowering plant species that provide the greatest proportion of the nectar sugar supply could also be used as proxies when modelling bee abundance against the nectar sugar supply. The species contributing the greatest proportion of the nectar sugar supply could therefore be targeted in future remote-sensing programmes. However, additional research would be needed to identify the flowering plant species that provide the greatest proportion of the nectar sugar supply across arable field margins in different regions of the UK.

Furthermore, while I specifically focused upon the availability of nectar sugar within an agricultural landscape, this is only one layer of many that need to be considered when managing resources for pollinators at a whole-farm scale. The spatial and temporal availability of other floral resources such as pollen, or within-resource variables such as macronutrient ratios, are also important to consider in future studies (e.g. Hanley et al., 2008; Vaudo et al., 2016; Vaudo et al., 2020), as are the accessibility of resources according to different pollinator groups (Goulnik, et al., 2021; Stang et al., 2006).

Nonetheless, I have developed a means of mapping nectar-rich flowering plant species that could have enormous benefits for on-farm pollinator conservation. Applications include identifying temporal and spatial resource gaps that can then be addressed through management changes or agri-environmental interventions, either separately or in conjunction with decision-support tools. Alternatively, classifications could be used as a layer within spatially-explicit models that predict pollinator richness, abundance or pollination services (e.g. Gardner et al., 2020; Lonsdorf et al., 2009). Furthermore, as agri-environment policy shifts towards a results-based focus, providing a means of mapping pollinator foraging resources remotely could prove a useful technique into the future as a way of monitoring biodiversity outcomes.

References

Abdel-Rahman, E.M., Makori, D.M., Landmann, T., Piiroinen, R., Gasim, S., Pellikka, P. and Raina, S.K. (2015). 'The Utility of AISA Eagle Hyperspectral Data and Random Forest Classifier for Flower Mapping', *Remote Sensing*, pp. 13298-13318. DOI: 10.3390/rs71013298

Agisoft. (2019). *Metashape – photogrammetric processing of digital images and 3D spatial data generation*. [online] Available at: <https://www.agisoft.com/> [Accessed: 12 June 2020].

Ahlmer, A-K., Cavalli, M., Hansson, K., Koutsouris, A.J., Crema, S. and Kalantari, Z. (2018). 'Soil moisture remote-sensing applications for identification of flood-prone areas along transport infrastructure', *Environmental Earth Sciences*, 77, Article 533, pp. 1-17. DOI: 10.1007/s12665-018-7704-z.

Akbar, K.F., Hale, W.H.G. and Headley, A.D. (2003). 'Assessment of scenic beauty of the roadside vegetation in northern England', *Landscape and Urban Planning*, 63(3), pp. 139-144. DOI: 10.1016/S0169-2046(02)00185-8.

Alaux, C., Ducloz, F., Crauser, D. and Le Conte, Y. (2010) 'Diet effects on honeybee immunocompetence', *Biology Letters*, 6 (4), pp. 562-565. DOI: 10.1098/rsbl.2009.0986.

Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw B.R., Bommarco, R., Campbell, A.J., Dainese, M., Drummond, F.A., Entling, M.H., Ganser, D., de Groot, G.A., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson,M., Knop, E., Kremen, C., Landis, D.A., Loeb, G.M., Marini, L., McKerchar, M., Morandin, L., Pfister, S.C., Potts, S.G., Rundlof, M., Sardiñas, H., Sciligo, A., Thies, C., Tscharntke, T., Venturini, E., Veromann, E., Vollhardt, I.M.G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S. and Sutter, L. (2021). 'The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: a quantitative synthesis', *Ecology Letters*, 23(10), pp. 1488-1498. DOI: 10.1111/ele.13576.

Andersson, S. (2008). 'Pollinator and nonpollinator selection on ray morphology in *Leucanthemum vulgare* (oxeye daisy, Asteraceae)', *American Journal of Botany*, 95(9), pp. 1072-1078. DOI: 10.3732/ajb.0800087.

Antoine, C.M. and Forrest, J.R.K. (2020). 'Nesting habitat of ground-nesting bees: a review', *Ecological Entomology*, 46(2), pp. 143-159. DOI: 10.1111/een.12986.

Artz, D.R., Hsu, C.L. and Nault, B.A. (2011). 'Influence of Honey Bee, *Apis mellifera*, Hives and Field Size on Foraging Activity of Native Bee Species in Pumpkin Fields, *Environmental Entomology*, 40(5), pp. 1144–1158. DOI: 10.1603/EN10218.

Asner, G.P., Jones, M.O., Martin, R.E., Knapp, D.E. and Hughes, R.F. (2008). 'Remote sensing of native and invasive species in Hawaiian forests', *Remote Sensing of Environment*, 112(5), pp. 1912-1926. DOI: 10.1016/j.rse.2007.02.043.

Bailes, E.J., Pattrick, J.G. and Glover, B.J. (2018). 'An analysis of the energetic reward offered by field bean (Vicia faba) flowers: Nectar, pollen, and operative force', *Ecology and Evolution*, 8(6), pp. 3161-3171. DOI: 10.1002/ece3.3851.

Baldridge, A.M., Hook, S.J., Grove, C.I. and Rivera, G. (2009). 'The ASTER spectral library version 2.0', *Remote Sensing of Environment*, 113(4), pp. 711-715. DOI: 10.1016/j.rse.2008.11.007.

Balfour, N.J., Ollerton, J., Castellanos, M.C. and Ratnieks, F.L.W. (2018). 'British phenological records indicate high diversity and extinction rates among late-summer-flying pollinators', *Biological Conservation*, 222, pp. 278-283. DOI: 10.1016/j.biocon.2018.04.028.

Barnas, A.F., Darby, B.J., Vandeberg, G.S., Rockwell, R.F. and Ellis-Felege, S.N. (2019). 'A comparison of drone imagery and ground-based methods for estimating the extent of habitat destruction by lesser snow geese (*Anser caerulescens caerulescens*) in La Pérouse Bay. *PLoS ONE*, 14(8), pp. 1-19 (e0217049). DOI: 10.1371/journal.pone.0217049

Bartomeus, I., Ascher, J.S., Wagner, D., Danforth, B.N., Colla, S., Kornbluth, S. and Winfree, R. (2011). 'Climate-associated phenological advances in bee pollinators and bee-pollinated plants', *PNAS*, 108(51), pp. 20645-20649. DOI: 10.1073/pnas.1115559108.

Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M. and Winfree, R. (2013). 'Historical changes in northeastern US bee pollinators related to shared ecological traits', *PNAS*, 110(12), pp. 4656-4660. DOI: 10.1073/pnas.1218503110.

Basari, N., Ramli, S.N., Abdul-Mutalid, N.A., Shaipulah, N.F.M. and Hashim, N.A. (2021). 'Flowers morphology and nectar concentration determine the preferred food source of stingless bee, *Heterotrigona itama*', *Journal of Asia-Pacific Entomology*, 24(2), pp. 232-236. DOI:

Baude, M., Kunin, W.E. and Memmott, J. (2015a). 'Nectar sugar values of common British plant species [AgriLand]'. NERC Environmental Information Data Centre. DOI: 10.5285/69402002-1676-4de9-a04e-d17e827db93c.

Baude, M., Kunin, W.E., Memmott, J. (2015b). 'Flower density values of common British plant species [AgriLand]'. NERC Environmental Information Data Centre. DOI: 10.5285/6c6d3844-e95a-4f84-a12e-65be4731e934.

Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., and Memmott, J. (2016) 'Historical nectar assessment reveals the fall and rise of floral resources in Britain', *Nature*, 530, pp. 85-88. DOI: 10.1038/nature16532.

Becher, M.A., Grimm, V., Thorbek, P., Horn, J., Kennedy, P.J. and Osborne, J.L. (2014). 'BEEHAVE: a systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure', *Journal of Applied Ecology*, 51 (2), pp. 470-482. DOI: 10.1111/1365-2664.12222.

Becher, M.A., Twiston-Davies, G., Penny, T.D., Goulson, D., Rotheray, E.L., and Osborne, J.L. (2018). '*Bumble*-BEEHAVE: A systems model for exploring multifactorial causes of bumblebee decline at individual, colony, population and community level', *Journal of Applied Ecology*, 55(6), pp. 2790-2801. DOI: 10.1111/1365-2664.13165.

Bedford, F.E., Whittaker, R.J. and Kerr, J.T. (2012). 'Systemic range shift lags among a pollinator species assemblage following rapid climate change', *Botany*, 90(7), pp. .DOI: 10.1139/b2012-052

Beekman, M. and Ratnieks, F.L.W. (2000). 'Long-range foraging by the honey-bee, *Apis mellifera* L.', *Functional Ecology*, 14(4), pp. 490-496. DOI: 10.1046/j.1365-2435.2000.00443.x.

Bégué, A., Arvor, D., Bellon, B., Betbeder, J., de Abelleyra, D., Ferraz, R.P.D., Lebourgeois, V., Lelong, C., Simões, M. and Verón, S.R. (2018). 'Remote Sensing and Cropping Practices: A Review', *Remote Sensing*, 10 (1), 99, pp. 1-32. DOI: 10.3390/rs10010099

Belgiu, M. and Drăguţ, L. (2016). 'Random forest in remote sensing: A review of applications and future directions', *ISPRS Journal of Photogrammetry and Remote Sensing*, 114 pp. 24-31. DOI: 10.1016/j.isprsjprs.2016.01.011

Berk, A., Bernstein, L.S., Anderson, G.P., Acharya, P.K., Robertson, D.C., Chetwynd, J.H. and Adler-Golden, S.M. (1998). 'MODTRAN Cloud and Multiple Scattering Upgrades with Application to AVIRIS', *Remote Sensing of Environment*, 65(3), pp. 367–375. DOI: 10.1016/S0034-4257(98)00045-5.

Betbeder, J., Hubert-Moy, L., Burel, F., Corgne, S. and Baudry, J. (2015) 'Assessing ecological habitat structure from local to landscape scales using synthetic aperture radar', *Ecological Indicators*, (52), pp. 545-557. DOI: 10.1016/j.ecolind.2014.11.009.

Biesmeijer, J.C. and Seeley, T.D. (2005). ‘The use of waggle dance information by honey bees throughout their foraging careers’, *Behavioral Ecology and Sociobiology*, 59, pp. 133–142.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. and Kunin, W.E. (2006) ‘Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands’, *Science*, 313 (5785), pp. 351-354. DOI: 10.1126/science.1127863.

Blaauw, B.R. and Isaacs, R. (2014). ‘Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop’, *Journal of Applied Ecology*, 51(4), pp. 890-898. DOI: 10.1111/1365-2664.12257.

Blaix, C. and Moonen, A-C. (2020). ‘Structural field margin characteristics affect the functional traits of herbaceous vegetation’, *PLoS ONE*, 15(9) pp. 1-21 (e0238916). DOI: 10.1371/journal.pone.0238916.

Bommarco, R., Lindström, S.A.M., Raderschall, C.A., Gagic, V. and Lundin, O. (2021). ‘Flower strips enhance abundance of bumble bee queens and males in landscapes with few honey bee hives’, *Biological Conservation*, 263, pp. 1-8 (109363). DOI: 10.1016/j.biocon.2021.109363.

Boston Seeds. (2021). ‘CSS3 Wildflower Meadow, also suitable for AB8’, URL: <https://www.bostonseeds.com/products/countryside-stewardship/countryside-stewardship-seed/css3-wildflower-meadow-also-suitable-for-ab8.html> [Accessed: 27/09/2021].

Bottero, I., Hodge, S., and Stout, J. (2021). Taxon-specific temporal shifts in pollinating insects in mass-flowering crops and field margins in Ireland. *Journal of Pollination Ecology*, *28*, 90–107. https://doi.org/10.26786/1920-7603(2021)628

Bradter, U., O’Connell, J., Kunin, W.E., Boffey, C.W.H., Ellis, R.J. and Benton, T.G. (2020). ‘Classifying grass-dominated habitats from remotely sensed data: The influence of spectral resolution, acquisition time and the vegetation classification system on accuracy and thematic resolution’, *Science of the Total Environment*, 711, pp. 1-14. DOI: 10.1016/j.scitotenv.2019.134584.

Breiman, L. (2001). ‘Random Forests’, *Machine Learning*, 45, pp. 5-32. DOI: 10.1023/A:1010933404324

Broadhead, G.T. and Raguso, R.A. (2021). ‘Associative learning of non-sugar nectar components: amino acids modify nectar preference in a hawkmoth’, *Journal of Experimental Biology*, 224 (12), pp. 1-9. DOI: 10.1242/jeb.234633.

Brodschneider, R. and Crailsheim, K. (2010). 'Nutrition and health in honey bees', *Apidologie*, 41, pp. 278–294. DOI: 10.1051/apido/2010012.

Burnett, C. and Blaschke, T. (2003). 'A multi-scale segmentation/object relationship modelling methodology for landscape analysis', *Ecological Modelling*, 168(3), pp. 233-249. DOI: 10.1016/S0304-3800(03)00139-X.

Cane, J.H., Griswold, T. and Parker, F.D. (2007). 'Substrates and Materials Used for Nesting by North American *Osmia* Bees (Hymenoptera: Apiformes: Megachilidae)', *Annals of the Entomological Society of America*, 100 (3), pp.350-358. DOI: 10.1603/0013-8746(2007)100[350:SAMUFN]2.0.CO;2.

Carey, P.D., Wallis, S., Chamberlain, P.M., Cooper, A., Emmett, B.A., Maskell, L.C., McCann, T., Murphy, J., Norton, L.R., Reynolds, B., Scott, W.A., Simpson, I.C., Smart, S.M. and J.M. Ullyett (2008). *Countryside Survey: UK Results from 2007*. Centre for Ecology and Hydrology.

Carl, C., Landgraf, D., van der Maaten-Theunissen, M., Biber, P. and Pretzsch, H. (2017). '*Robinia pseudoacacia* L. Flower Analyzed by Using an Unmanned Aerial Vehicle (UAV)', *Remote Sensing*, 9 (11), pp. 1-19. DOI: 10.3390/rs9111091.

Carreck N.L., Williams I.H. and Oakley J.N. (1999) Enhancing farmland for insect pollinators using flower mixtures. *Aspects of Applied Biology*, 54, pp. 101-108.

Carreck, N.L. and Williams, I.H. (2002). 'Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures', *Journal of Insect Conservation*, 6, pp. 13–23. DOI: 10.1023/A:1015764925536.

Carrié, R., Lopes, M., Ouin, A. and Andrieu, E. (2018). 'Bee diversity in crop fields is influenced by remotely-sensed nesting resources in surrounding permanent grasslands' *Ecological Indicators*, 90, pp. 606–614. DOI: 10.1016/j.ecolind.2018.03.054.

Carvalheiro, L. G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Hennekens, S., Landuyt, W.V., Maes, D., deMeutter, F.V., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M, Schaminée, J., WallisDeVries, M.F. and Biesmeijer, J.C. (2013). 'Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants', *Ecology Letters*, 16 (7), pp. 870–878. DOI: 10.1111/ele.12121.

Carvalho, S., Schlerf, M., van der Putten, W.H., Skidmore, A.K. (2013). 'Hyperspectral reflectance of leaves and flowers of an outbreak species discriminates season and successional stage of vegetation', *International Journal of Applied Earth Observation and Geoinformation*, pp. 32-41. DOI: 10.1016/j.jag.2013.01.005.

Carvell, C., Meek, W.R., Pywell, R.F. and Nowakowski, M. (2004). 'The response of foraging bumblebees to successional change in newly created arable field margins', *Biological Conservation*, 118 (3), pp. 327–339. DOI: 10.1016/j.biocon.2003.09.012.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. and Goulson, D. (2006a). 'Declines in forage availability for bumblebees at a national scale', *Biological Conservation*, 132, pp. 481 – 489. DOI: 10.1016/j.biocon.2006.05.008.

Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F. and Nowakowski, M. (2006b). 'Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis', *Apidologie*, 37 (3), pp. 326-340. DOI: 10.1051/apido:2006002.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. and Nowakowski, M. (2007). 'Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins', *Journal of Applied Ecology*, 44 (1), pp. 29-40. DOI: 10.1111/j.1365-2664.2006.01249.x.

Carvell, C., Bourke, A.F.G., Dreier, S., Freeman, S.N., Hulmes, S., Jordan, W.C., Redhead, J.W., Sumner, S., Wang, J. and Heard, M.S. (2017). 'Bumblebee family lineage survival is enhanced in high-quality landscapes', *Nature*, 543 (7646), pp. 547-549. DOI: 10.1038/nature21709.

Chaplin, S.P., Mills, J. and Chiswell, H. (2021). 'Developing payment-by-results approaches for agri-environment schemes: Experience from an arable trial in England', *Land Use Policy*, 109, pp. 1-12 (105698) DOI: 10.1016/j.landusepol.2021.105698.

Chen, J., Shen, M., Zhu, X. and Tang, Y. (2009). 'Indicator of flower status derived from in situ hyperspectral measurement in an alpine meadow on the Tibetan Plateau', *Ecological Indicators*, 9, pp. 818–823. DOI: 10.1016/j.ecolind.2008.09.009.

Clay, G.R. and Daniel, T.C. (2000). 'Scenic landscape assessment: the effects of land management jurisdiction on public perception of scenic beauty', *Landscape and Urban Planning*, 49(1-2), pp. 1-13. DOI: 10.1016/S0169-2046(00)00055-4.

Cnaani, J., Thomson, J.D. and Papaj, D.R. (2006). 'Flower Choice and Learning in Foraging Bumblebees: Effects of Variation in Nectar Volume and Concentration', *Ethology*, 112(3), pp. 278-285. DOI: 10.1111/j.1439-0310.2005.01174.x.

Cole, L.J., Kleijn, D., Dicks, L.V., Stout, J.C., Potts, S.G., Albrecht, M., Balzan, M.V., Bartomeus, I., Bebeli, P.J., Bevk, D., Biesmeijer, J.C., Chlebo, R., Dautarte, A., Emmanouil, N., Hartfield, C., Holland, J.M., Holzschuh, A., Knoben, N.T.J., Kovacs-Hostyanszki, A., Mandelik, Y., Panou, H., Paxton, R.J., Petanidou, T., de Carvalho, M.A.A.P., Rundlof, M., Sarthou, J.P., Stavrinides, M.C., Suso, M.J., Szentgyorgyi, H., Vaissiere, B.E., Varnava, A., Vila, M., Zemeckis, R. and Scheper, J. (2020). 'A critical analysis of the potential for EU Common Agricultural Policy measures to support wild pollinators on farmland'. *Journal of Applied Ecology*, 57 (4), pp. 681-694. DOI: 10.1111/1365-2664.13572.

Congedo, L. (2016). *Semi-Automatic Classification Plugin*. Version 6.4.0 [computer program].
Congedo, L. (2021). 'Semi-Automatic Classification Plugin 7.9.7.1 documentation', URL: <https://semiautomaticclassificationmanual.readthedocs.io/en/latest/index.html> [Accessed: 07/11/2022].

Couvillon, M.J., Riddell Pearce, F.C., Accleton, C., Fensome, K.A., Quah, S.K.L., Taylor, E.L. and Ratnieks, F.L.W. (2015). 'Honey bee foraging distance depends on month and forage type', *Apidologie*, 46, pp. 61–70. DOI: 10.1007/s13592-014-0302-5.

Crawley, M.J. (2005). *Statistics : an introduction using R*. Chichester, England: John Wiley & Sons, Ltd.

Cresswell, J.E. (1999). 'The influence of nectar and pollen availability on pollen transfer by individual flowers of oil-seed rape (Brassica napus) when pollinated by bumblebees (Bombus lapidarius)', Journal of Ecology, 87(4), pp. 670-677. DOI: 10.1046/j.1365-2745.1999.00385.x.

Cresswell, C.J., Cunningham, H.M., Wilcox, A. and Randall, N.P. (2019). 'A trait-based approach to plant species selection to increase functionality of farmland vegetative strips', *Ecology and Evolution*, 9(8), pp. 4532-4543. DOI: 10.1002/ece3.5047.

Critchley, C.N.R., Fowbert, J.A., Sherwood, A.J. and Pywell, R.F. (2006). 'Vegetation development of sown grass margins in arable fields under a countrywide agri-environment scheme', *Biological Conservation*, 132 (1), DOI: 10.1016/j.biocon.2006.03.007.

Dailey, T.B. and Scott, P.E. (2006). 'Spring Nectar Sources for Solitary Bees and Flies in a Landscape of Deciduous Forest and Agricultural Fields: Production, Variability, and Consumption', *The Journal of the Torrey Botanical Society*, 133(4), pp. 535-547.DOI: 10.3159/1095-5674(2006)133[535:SNSFSB]2.0.CO;2.

Daponte, P., De Vito, L., Glielmo, L., Iannelli, L., Liuzza, D., Picariello, F. and Silano, G. (2019). 'A review on the use of drones for precision agriculture', *IOP Conference Series: Earth and Environmental Science*, 275, pp. 1-10 (012022). DOI: 10.1088/1755-1315/275/1/012022.

Dash, J.P., Watt, M.S., Paul, T.S.H., Morgenroth, J. and Pearse, G.D. (2019). 'Early Detection of Invasive Exotic Trees Using UAV and Manned Aircraft Multispectral and LiDAR Data', *Remote Sensing*, 11 (15), pp. 1-21. DOI: 10.3390/rs11151812.

De Sá, N.C., Castro, P., Carvalho, S., Marchante, E., López-Núñez, F.A. and Marchante H. (2018). 'Mapping the Flowering of an Invasive Plant Using Unmanned Aerial Vehicles: Is There Potential for Biocontrol Monitoring?', *Frontiers in Plant Science*, 9(293), pp. 1-13. DOI: 10.3389/fpls.2018.00293.

Defra. (2013). Entry Level Stewardship (ELS) Handbook 2013 (NE349) URL: <http://adlib.everysite.co.uk/adlib/defra/content.aspx?id=2RRVTHNXTS.987E8CZTGNT2O> [Accessed: 01/12/2021]

Delavarpour, N., Koparan, C., Nowatzki, J., Bajwa, S. and Sun, X. (2021). 'A Technical Study on UAV Characteristics for Precision Agriculture Applications and Associated Practical Challenges', *Remote Sensing*, 13, 1204. DOI:10.3390/rs13061204.

Dicks, L.V., Baude, M., Roberts, S.P.M., Phillips, J., Green, M. and Carvell, C., (2015). 'How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge', *Ecological Entomology*, 40, (Suppl. 1), pp. 22–35. DOI: 10.1111/een.12226.

Dicks, L.V., Breeze, D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J. and Potts, S.G. (2021). 'A global-scale expert assessment of drivers and risks associated with pollinator decline', *Nature Ecology and Evolution*, 5, pp. 1453–1461. DOI: 10.1038/s41559-021-01534-9.

Di Pasquale, G., Salignon, M., Le Conte, Y., Belzunces, L.P., Decourtye, A., Kretzschmar, A., Suchail, S., Brunet, J-L and Alaux, C. (2013). 'Influence of Pollen Nutrition on Honey Bee Health: Do Pollen Quality and Diversity Matter?', *PLoS ONE*, 8(8), pp. 1-13 (e72016). DOI: 10.1371/journal.pone.0072016.

Elliot, S.E. (2009). ‘Surplus Nectar Available for Subalpine Bumble Bee Colony Growth’, *Environmental Entomology*, 38 (6), pp. 1680–1689. DOI: 10.1603/022.038.0621.

Emorsgate Seeds. (2021). ‘EM1 – Basic General Purpose Meadow Mixture’, URL: < https://wildseed.co.uk/mixtures/view/2/basic-general-purpose-meadow-mixture> [Accessed: 27/09/2021].

ESA (2021). ‘Overview’, <URL:https://sentinel.esa.int/web/sentinel/missions/sentinel-2/overview> [Accessed: 29/10/2021].

Everitt, J.H., Yang, C. and Davis, M.R. (2007). ‘Mapping Wild Taro with Color-infrared Aerial Photography and Image Processing’, *Journal of Aquatic Plant Management*, 45 (2), pp. 106-110.

Fang H. and Liang, S. (2008). ‘Leaf Area Index Models’, *Encyclopedia of Ecology*, pp. 2139-2148. DOI: 10.1016/B978-0-12-409548-9.09076-X.

Feilhauer, H., Thonfeld, F., Faude, U., He, K.S., Rocchini, D. and Schmidtlein, S. (2013). ‘Assessing floristic composition with multispectral sensors – A comparison based on monotemporal and multiseasonal field spectra’, *International Journal of Applied Earth Observation and Geoinformation*, 21, pp. 218-229. DOI: 10.1016/j.jag.2012.09.002.

Feilhauer, H., Doktor, D., Schmidtlein, S., and Skidmore, A.K. (2016). ‘Mapping pollination types with remote sensing’, *Journal of Vegetation Science*, 27, pp. 999-1011. DOI: 10.1111/jvs.12421.

Feltham, H., Park, K., Minderman, J. and Goulson, D. (2015). ‘Experimental evidence that wildflower strips increase pollinator visits to crops’, *Ecology and Evolution*, 5(16), pp. 3523-3530. DOI: 10.1002/ece3.1444.

Feng, Q., Liu, J. and Gong, J. (2015). ‘UAV Remote Sensing for Urban Vegetation Mapping Using Random Forest and Texture Analysis’, *Remote Sensing*, 7(1), pp. 1074-1094. DOI: 10.3390/rs70101074. Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. and Thomson, J.D. (2004). ‘Pollination Syndromes and Floral Specialization’, *Annual Review of Ecology, Evolution, and Systematics*, 35, pp. 375-403. DOI: 10.1146/annurev.ecolsys.34.011802.132347.

Fisher, J.R.B., Acosta, E.A., Dennedy-Frank, P.J., Kroeger, T. and Boucher, T.M. (2018). ‘Impact of satellite imagery spatial resolution on land use classification accuracy and modeled water quality’, *Remote Sensing in Ecology and Conservation*, 4 (2), pp. 137-149. DOI: 10.1002/rse2.61.

Flo, V., Bosch, J., Arnan, X., Primante, C., Martín González, A.M., Barril-Graells, H. and Rodrigo, A. (2018). ‘Yearly fluctuations of flower landscape in a Mediterranean scrubland: Consequences for floral resource availability’, *PLoS ONE*, 13(1), pp. (e0191268). DOI: 10.1371/journal.pone.0191268.

Foody, G.M. (2008). ‘Harshness in image classification accuracy assessment’, *International Journal of Remote Sensing*, 29 (11), pp. 3137–3158. DOI: 10.1080/01431160701442120

Foody, G.M. (2020). ‘Explaining the unsuitability of the kappa coefficient in the assessment and comparison of the accuracy of thematic maps obtained by image classification’, *Remote Sensing of Environment*, 239, pp. 1-11. DOI: 10.1016/j.rse.2019.111630.

Foody, G.M. and Arora, M.K. (1996). ‘Incorporating mixed pixels in the training, allocation and testing stages of supervised classifications’, *Pattern Recognition Letters,* 17 (13), pp. 1389-1398. DOI: 10.1016/S0167-8655(96)00095-5.

Fornoff, F., Klein, A-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M. and Ebeling, A. (2017). ‘Functional flower traits and their diversity drive pollinator visitation’, *Oikos*, 126 (7), pp. 1020–1030. DOI: 10.1111/oik.03869.

FReD (2021). ‘Welcome to FReD’ <http://www.reflectance.co.uk//index.php> [Accessed: 15/12/2021]

Fretwell, P.T. and Trathan, P.N. (2021). ‘Discovery of new colonies by Sentinel2 reveals good and bad news for emperor penguins’, *Remote Sensing in Ecology and Conservation*, 7 (2), pp. 139-153. DOI: 10.1002/rse2.176.

Fritz, A., Li, L., Storch, I. and Koch, B. (2018) ‘UAV-derived habitat predictors contribute strongly to understanding avian species–habitat relationships on the Eastern Qinghai-Tibetan Plateau’, *Remote Sensing in Ecology and Conservation*, 4 (1), pp. 53–65. DOI: 10.1002/rse2.73.

Frontier Agriculture Ltd. (2021). ‘Basic Pollen and Nectar Mix KWM2bs’, URL: <https://www.kingscrops.co.uk/products/product/18-basic-pollen-and-nectar-mix> [Accessed: 27/09/2021].

Gabriel, D. and Tscharntke, T. (2007). ‘Insect pollinated plants benefit from organic farming’, *Agriculture, Ecosystems & Environment*, 118(1-4), pp. 43-48. DOI: 10.1016/j.agee.2006.04.005.

Galbraith, S.M., Vierling, L.A. and Bosque-Pérez, N.A. (2015). ‘Remote Sensing and Ecosystem Services: Current Status and Future Opportunities for the Study of Bees and Pollination-Related Services’, *Current Forestry Reports*, 1, pp. 261–274. DOI: 10.1007/s40725-015-0024-6.

Garbuzov, M., Balfour, N.J., Shackleton, K., Al Toufailia, H., Scandian, L. and Ratnieks, F.L.W. (2020). ‘Multiple methods of assessing nectar foraging conditions indicate peak foraging difficulty in late season’, *Insect Conservation and Diversity*, 13(6), pp. 532-542. DOI: 10.1111/icad.12420.

Gardner, E., Breeze, T.D., Clough, Y., Smith, H.G., Baldock, K.C.R., Campbell, A., Garratt, M.P.D., Gillespie, M.A.K., Kunin, W.E., McKerchar, M., Memmott, J., Potts, S.G., Senapathi, D., Stone, G.N., Wäckers, F., Westbury, D.B., Wilby, A. and Oliver, T.H. (2020). 'Reliably predicting pollinator abundance: Challenges of calibrating process-based ecological models', *Methods in Ecology and Evolution*, 11 (12), pp. 1673-1689. DOI: 10.1111/2041-210X.13483.

Garratt, M.P.D., Senapathi, D., Coston, D.J., Mortimer, S.R. and Potts, S.G. (2017). 'The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context', *Agriculture, Ecosystems & Environment*, 247, pp. 363-370. DOI: 10.1016/j.agee.2017.06.048.

Gathmann, A. and Tscharntke, T. (2002). 'Foraging ranges of solitary bees', *Journal of Animal Ecology*, 71(5), pp. 757-764. DOI: 10.1046/j.1365-2656.2002.00641.x

Ge, S., Everitt, J., Carruthers, R., Gong, P. and Anderson, G. (2006). 'Hyperspectral Characteristics of Canopy Components and Structure for Phenological Assessment of an Invasive Weed', *Environmental Monitoring and Assessment*, 120, pp. 109–126. DOI: 10.1007/s10661-005-9052-1

Gebhardt, S., Schellberg, J., Lock, R. and Kühbauch, W. (2006). 'Identification of broad-leaved dock (*Rumex obtusifolius* L.) on grassland by means of digital image processing', *Precision Agriculture*, 7, pp. 165–178. DOI: 10.1007/s11119-006-9006-9.

Gedminas, L. and Martin, S. (2019). Soil Organic Matter Mapping Using Hyperspectral Imagery and Elevation Data. In: *2019 IEEE Aerospace Conference*, 2-9 March 2019, Big Sky, MT, USA, IEEE, pp.1-8. DOI: 10.1109/AERO.2019.8741728.

Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Fontaine, C., Henry, M., Ropars, L., Rollin, O., Thébault, E. and Vereecken, N.J. (2017). 'Chapter Four - Massively Introduced Managed Species and Their Consequences for Plant–Pollinator Interactions', *Advances in Ecological Research*, 57, pp.147-199. DOI: 10.1016/bs.aecr.2016.10.007.

Gholizadeh, A., Žižala, D., Saberioon, M. and Borůvkaa, L. (2018). 'Soil organic carbon and texture retrieving and mapping using proximal, airborne and Sentinel-2 spectral imaging', *Remote Sensing of Environment*, 218, pp. 89-103. DOI: 10.1016/j.rse.2018.09.015.

Ghosh, S., Jeon, H. and Jung, C. (2020). 'Foraging behaviour and preference of pollen sources by honey bee (*Apis mellifera*) relative to protein contents', *Journal of Ecology and Environment*, 44(4), pp. 1-7. DOI: 10.1186/s41610-020-0149-9.

Goidts, E. and van Wesemael, B. (2007). ‘Regional assessment of soil organic carbon changes under agriculture in Southern Belgium (1955–2005)’, *Geoderma*, 141 (3–4), pp. 341-354. DOI: 10.1016/j.geoderma.2007.06.013.

Gómez, C., White, J.C. and Wulder, M.A. (2016). ‘Optical remotely sensed time series data for land cover classification: A review’, *ISPRS Journal of Photogrammetry and Remote Sensing,*

116, pp. 55-72. DOI: 10.1016/j.isprsjprs.2016.03.008

Gong, P. and Howarth, P.J., (1990). ‘The Use of Structural Information for Improving Land-Cover Classification Accuracies at the Rural-Urban Fringe’, *Photogrammetric Engineering and Remote Sensing*, 56 (1), pp. 67-73. DOI: 0099-1112/90/5601-67$02.25/0.

González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., Potts, S.G., Schweiger, O., Smith, H.G., Steffan-Dewenter, I., Szentgyörgyi, H., Woyciechowski, M. and Vilà, M. (2013). ‘Combined effects of global change pressures on animal-mediated pollination’, *Trends in Ecology and Evolution*, 28(9), pp. 524-530. DOI: 10.1016/j.tree.2013.05.008.

Google Earth Pro V 7.3.4.8642 (2015). *United Kingdom and Republic of Ireland, 54°36’44.91”N, 3°35’42.17”W, Eye alt 1604.89km,* Data SIO, NOAA, U.S. Navy, NGA, GEBCO, Image Landsat / Copernicus.

Google Earth Pro V 7.3.4.8642 (2020a). *Near Mears Ashby / Whiston, Northamptonshire, UK, 52°16’11.70”N, 0°44’58.87”W, Eye alt 16.49km.*

Google Earth Pro V 7.3.4.8642 (2020b). *Near Mears Ashby, Northamptonshire, UK, 52°18’05.28”N, 0°45’42.54”W, Eye alt 4.23km.*

Google Earth Pro V 7.3.4.8642 (2020c). *Near Whiston, Northamptonshire, UK, 52°13’49.84”N, 0°46’11.86”W, Eye alt 3.06km.*

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. and Knight, M.E. (2005) ‘Causes of rarity in bumblebees’, *Biological Conservation*, 122, pp. 1-8.

Goulnik, J., Plantureux, S., Dajoz, I. and Michelot-Antalik, A. (2021). ‘Using Matching Traits to Study the Impacts of Land-Use Intensification on Plant–Pollinator Interactions in European Grasslands: A Review’, *Insects*, 12(8), pp. 1-16 (680). DOI: 10.3390/insects12080680.

Goulson, D., Lye, G.C. and Darvill, B. (2008). ‘Decline and Conservation of Bumble Bees’, *Annual Review of Entomology*, 53, pp. 191-208. DOI: 10.1146/annurev.ento.53.103106.093454.

Goulson, D. (2010). ‘Bumblebees: Behaviour, Ecology, and Conservation’, 2nd ed. Oxford University Press: Oxford.

Goulson, D., Nicholls, E., Botías, C. and Rotheray, E.L. (2015). ‘Bee declines driven by combined stress from parasites, pesticides, and lack of flowers’, *Science*, 347 (6229), pp. 1-9. DOI: 10.1126/science.1255957.

Goyret, J., Pfaff, M., Raguso, R.A. and Kelber, A. (2008). ‘Why do *Manduca sexta* feed from white flowers? Innate and learnt colour preferences in a hawkmoth’, *Naturwissenschaften*, 95, pp. 569-576. DOI: 10.1007/s00114-008-0350-7.

Gradish, A.E., van der Steen, J., Scott-Dupree, C.D., Cabrera, A.R., Cutler, C., Goulson, D., Klein, O., Lehmann, D.M., Lückmann, J., O’Neill, B., Raine, N.E., Sharma, B. and Thompson, H. (2018). ‘Comparison of Pesticide Exposure in Honey Bees (Hymenoptera: Apidae) and Bumble Bees (Hymenoptera: Apidae): Implications for Risk Assessments’, *Environmental Entomology*, 48(1), pp. 1-10. DOI: 10.1093/ee/nvy168.

Greenleaf, S.S., Williams, N.M., Winfree, R. and Kremen, C. (2007). ‘Bee foraging ranges and their relationship to body size’, *Oecologia*, 153, pp. 589–596. DOI: 10.1007/s00442-007-0752-9.

Gregory, S. and Wright I. (2005). ‘Creation of patches of bare ground to enhance the habitat of ground-nesting bees and wasps at Shotover Hill, Oxfordshire, England’, *Conservation Evidence*, 2, pp. 139-141.

Gresty, C.E.A., Clare, E., Devey, D.S., Cowan, R.S., Csiba, L., Malakasi, P., Lewis, O.T. and Willis, K.J. (2018). ‘Flower preferences and pollen transport networks for cavity-nesting solitary bees: Implications for the design of agri-environment schemes’, *Ecology and Evolution*, 8(15), pp. 7574-7587. DOI: 10.1002/ece3.4234.

Grinand, C.; Rakotomalala, F.; Gond, V.; Vaudry, R.; Bernoux, M. and Vieilledent, G. (2013). ‘Estimating deforestation in tropical humid and dry forests in Madagascar from 2000 to 2010 using multi-date Landsat satellite images and the random forests classifier’, *Remote Sensing of Environment*, 139, pp. 68-80. DOI: 10.1016/j.rse.2013.07.008.

Grixti, J.C., Wong, L.T., Cameron, S.A. and Favret, C. (2009). ‘Decline of bumble bees (Bombus) in the North American Midwest’, *Biological Conservation*, 142(1), pp. 75-84. DOI: 10.1016/j.biocon.2008.09.027.

Guezen, J.M. and Forrest, J.R.K. (2021). ‘Seasonality of floral resources in relation to bee activity in agroecosystems’, *Ecology and Evolution*, 11, pp.3130–3147. DOI: 10.1002/ece3.7260.

Guo, M.; Li, J.; Sheng, C.; Xu, J. and Wu, L. (2017). 'A Review of Wetland Remote Sensing', *Sensors*, 17 (4). DOI: 10.3390/s17040777.

Haaland, C. and Bersier, L-F. (2011). 'What can sown wildflower strips contribute to butterfly conservation?: an example from a Swiss lowland agricultural landscape', *Journal of Insect Conservation*, 15, pp. 301–309. DOI: 10.1007/s10841-010-9353-8.

Hanley, M.E., Franco, M., Pichon, S., Darvill, B. and Goulson, D. (2008). 'Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants', *Functional Ecology*, 22(4), pp. 592-598.

Harder, L.D. (1986). 'Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees', *Oecologia*, 69, pp. 309-315. DOI: 10.1007/BF00377639.

Häussler, J., Sahlin, U., Baey, C., Smith, H.G. and Clough, Y. (2017). 'Pollinator population size and pollination ecosystem service responses to enhancing floral and nesting resources', *Ecology and Evolution*, 7 (6), pp. 1898-1908. DOI: 10.1002/ece3.2765.

Heinrich, B. (1979). *Bumblebee economics*. Cambridge: Harvard University Press.

Hemberger, J., Crossley, M.S. and Gratton, C. (2021). 'Historical decrease in agricultural landscape diversity is associated with shifts in bumble bee species occurrence', *Ecology Letters*, 24(9), pp. 1800-1813. DOI: 10.1111/ele.13786.

Hennessy, G., Uthoff, C., Abbas, S., Quaradeghini, S.C., Stokes, E., Goulson, D. and Ratnieks, F.L.W. (2021). 'Phenology of the specialist bee *Colletes hederae* and its dependence on *Hedera helix* L. in comparison to a generalist, *Apis mellifera', Arthropod-Plant Interactions*, 15, pp. 183–195. DOI: 10.1007/s11829-021-09807-7

Henrys, P.A. and Jarvis, S.G. (2019). 'Integration of ground survey and remote sensing derived data: Producing robust indicators of habitat extent and condition', *Ecology and Evolution*, 9(14), pp. 8104–8112. DOI: 10.1002/ece3.5376.

HexCam. (2022). 'Aerial Surveys and Mapping', URL: <https://hexcam.co.uk/drone-surveys-mapping> [Accessed: 07/11/2022].

Hicks, D. M., Ouvrard, P., Baldock, K. C. R., Baude, M., Goddard, M. A., Kunin, W. E., Mitschunas, N., Memmott, J., Morse, H., Nikolitsi, M., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Sinclair, F., Westbury, D. B., and Stone, G. N. (2016). 'Food for pollinators: Quantifying the Nectar and Pollen Resources of Urban Flower Meadows', *PLoS ONE*, 11 (6): e0158117, pp. 1-37. DOI: 10.1371/journal.pone.0158117.

Holl, K. (1995). ‘Nectar Resources and Their Influence on Butterfly Communities on Reclaimed Coal Surface Mines’, *Restoration Ecology*, 3 (2), pp. 76-85. DOI: 10.1111/j.1526-100X.1995.tb00080.x.

Holland, J. and Aplin, P. (2013). ‘Super-resolution image analysis as a means of monitoring bracken (*Pteridium aquilinum*) distributions’, *ISPRS Journal of Photogrammetry and Remote Sensing*, 75, pp. 48-63. DOI: 10.1016/j.isprsjprs.2012.10.002.

Holland, J.M., Smith, B.M., Storkey, J., Lutman, P.J.W. and Aebischer, N.J. (2015). ‘Managing habitats on English farmland for insect pollinator conservation’, *Biological Conservation*, 182, pp. 215-222. DOI: 10.1016/j.biocon.2014.12.009.

Holland, J.M., Douma, J.C., Crowley, L., James, L., Kor, L., Stevenson, D.R.W. and Smith, B.M. (2017). ‘Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review’, *Agronomy for Sustainable Development*, 37(31), pp. 1-23. DOI: 10.1007/s13593-017-0434-x.

Holzschuh, A., Dormann, C.F., Tscharntke, T. and Steffan-Dewenter, I. (2011) ‘Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination’, *Proceedings of the Royal Society B*, 278 (1723), pp. 3444-3451, DOI: 10.1098/rspb.2011.0268.

Horning, N., Leutner, B. and Wegmann, M. (2016). Land Cover or Image Classification Approaches. In: Wegmann, M., Leutner, B. and Dech, S. eds. *Remote Sensing and GIS for Ecologists: Using Open Source Software*. Exeter, UK: Pelagic Publishing, pp.166-196.

Horton, R., Cano, E., Bulanon, D. Fallahi, E. (2017). ‘Peach Flower Monitoring Using Aerial Multispectral Imaging’, *Journal of Imaging*, 3 (1), pp. 1-10. DOI: 10.3390/jimaging3010002.

Hoyle, H., Norton, B., Dunnett, N., Richards, J.P., Russell, J.M., Warren, P. (2018). ‘Plant species or flower colour diversity? Identifying the drivers of public and invertebrate response to designed annual meadows’, *Landscape and Urban Planning*, 180, pp. 103-113. DOI: 10.1016/j.landurbplan.2018.08.017.

Hruska, R., Mitchell, J., Anderson, M. and Glenn, N.F. (2012). ‘Radiometric and Geometric Analysis of Hyperspectral Imagery Acquired from an Unmanned Aerial Vehicle’, *Remote Sensing*, 4, pp. 2736-2752. DOI: 10.3390/rs4092736.

Huang, Y., Thomson, S.J., Lan, Y. and Maas, S.J. (2010). ‘Multispectral imaging systems for airborne remote sensing to support agricultural production management’, *International Journal of*

Agricultural and Biological Engineering, 3(1), pp. 1-13, DOI: 10.3965/j.issn.1934-6344.2010.01.050-062.

Hutchinsons. (2021a). 'Hutchinsons Crop Production Specialists', URL: <https://www.hlhltd.co.uk> [Accessed: 23/07/2021].

Hutchinsons. (2021b). 'Omnia Precision Agronomy', URL: <https://www.hlhltd.co.uk/wp-content/uploads/2021/06/3397-Omnia-Brochure-Hutchinsons.pdf> [Accessed: 29/09/2021].

Ion, N., Odoux, J-F. and Vaissière, B.E. (2018). 'Melliferous Potential of Weedy Herbaceous Plants in Crop Fields of Romania from 1949 to 2012', *Journal of Apicultural Science*, 62(2), pp. 149-165. DOI: 10.2478/JAS-2018-0017.

Islam, K.; Jashimuddin, M.; Nath, B. and Nath, T. K. (2018). 'Land use classification and change detection by using multi-temporal remotely sensed imagery: The case of Chunati wildlife sanctuary, Bangladesh', *The Egyptian Journal of Remote Sensing and Space Science*, 21 (1), pp. 37-47. DOI: 10.1016/j.ejrs.2016.12.005.

Jachuła, J., Denisow, B. and Wrzesień, M. (2021). 'Habitat heterogeneity helps to mitigate pollinator nectar sugar deficit and discontinuity in an agricultural landscape', *Science of The Total Environment*, 782 (146909), pp. 1-14. DOI: 10.1016/j.scitotenv.2021.146909.

Jakob, S., Zimmermann, R. and Gloaguen, R. (2017). 'The Need for Accurate Geometric and Radiometric Corrections of Drone-Borne Hyperspectral Data for Mineral Exploration: MEPHySTo—A Toolbox for Pre-Processing Drone-Borne Hyperspectral Data', *Remote Sensing*, 9(1), pp. (88). DOI: 10.3390/rs9010088.

Johansen, L., Westin, A., When, S., Iuga, A., Ivascu, C.M., Kallioniemi, E., and Lennartsson, T. (2019). 'Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes', *Global Ecology and Conservation*, 18 (e00619), pp. 1-12. DOI: 10.1016/j.gecco.2019.e00619.

Kammerer, M., Goslee, S.C., Douglas, M.R., Tooker, J.F. and Grozinger, C.M. (2021). 'Wild bees as winners and losers: Relative impacts of landscape composition, quality, and climate', *Global Change Biology*, 27(6), pp. 1250-1265. DOI: 10.1111/gcb.15485.

Kämper, W., Werner, P.K., Hilpert, A., Westphal, C., Blüthgen, N., Eltz, T. and Leonhardt, S.D. (2016). 'How landscape, pollen intake and pollen quality affect colony growth in *Bombus terrestris*', *Landscape Ecology*, 31 (10), pp. 2245–2258. DOI: 10.1007/s10980-016-0395-5.

Kattenborn, T., Fassnacht, F.E. and Schmidtlein, S. (2019). 'Differentiating plant functional types using reflectance: which traits make the difference?', *Remote Sensing in Ecology and Conservation*, 5 (1), pp. 5–19. DOI: 10.1002/rse2.86.

Kells, A.R., Holland, J.M. and Goulson, D. (2001). 'The value of uncropped field margins for foraging bumblebees', *Journal of Insect Conservation*, 5, pp. 283–291. DOI: 10.1023/A:1013307822575.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R, Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhoffer, J-H, Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlof, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S. and Kremen, C. (2013). 'A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems', *Ecology Letters*, 16, pp. 584-599. DOI: 10.1111/ele.12082.

Kim, W., Gilet, T. and Bush, J.W.M. (2011). 'Optimal concentrations in nectar feeding', *Proceedings of the National Academy of Sciences of the United States of America*, 108 (40), pp. 16618-16621. DOI: 10.1073/pnas.1108642108.

Kleijn, D. and Snoeijing, G.I.J. (1997). 'Field Boundary Vegetation and the Effects of Agrochemical Drift: Botanical Change Caused by Low Levels of Herbicide and Fertilizer', *Journal of Applied Ecology*, 34(6), pp. 1413-1425. DOI: 10.2307/2405258.

Kleijn, D., Winfree, R., Bartomeus, I. et al. (2015) 'Delivery of crop pollination services is an insufficient argument for wild pollinator conservation', *Nature Communications*, 6 (7414), pp. 1-8. DOI: 10.1038/ncomms8414.

Klein, A-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I.,Cunningham, S.A., Kremen, C. and Tscharntke, T. (2007), 'Importance of pollinators in changing landscapes for world crops', *Proceedings of the Royal Society B*, 274 (1608), pp. 303-313. DOI: 10.1098/rspb.2006.3721

Klumpers, S.G.T., Stang, M. and Klinkhamer, P.G.L. (2019). 'Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length', *Ecology Letters*, 22(3), pp. 469-479. DOI: 10.1111/ele.13204.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, R.A. and Goulson, D. (2005). 'An interspecific comparison of foraging range and nest density of four bumblebee

(Bombus) species', *Molecular Ecology*, 14 (6), pp. 1811-1820. DOI: 10.1111/j.1365-294X.2005.02540.x

Kohler, F., Verhulst, J., Van Klink, R. and Kleijn, D. (2008). 'At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes?', *Journal of Applied Ecology*, 45(3), pp. 753-762. DOI: 10.1111/j.1365-2664.2007.01394.x.

Kokaly, R.F., Asner, G.P., Ollinger, S.V., Martin, M.E. and Wessman, C.A. (2009). 'Characterizing canopy biochemistry from imaging spectroscopy and its application to ecosystem studies', *Remote Sensing of Environment*, 113 (Supplement 1), pp. S78-S91, DOI:10.1016/j.rse.2008.10.018.

Kokaly, R.F., Clark, R.N., Swayze, G.A., Livo, K.E., Hoefen, T.M., Pearson, N.C., Wise, R.A., Benzel, W.M., Lowers, H.A., Driscoll, R.L., and Klein, A.J. (2017). *USGS Spectral Library Version 7*. U.S. Geological Survey Data Series 1035, 61. Reston, Virginia, USA: U.S. Geological Survey. DOI: 10.3133/ds1035.

Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Kro´l, W., Solarz W. and Płonka, P. (2007). 'The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe', *Oryx*, 41 (1), pp. 79-88. DOI: 10.1017/S0030605307001597.

Krimmer, E., Martin, E.A., Krauss, J., Holzschuh, A. and Steffan-Dewenter, I. (2019). 'Size, age and surrounding semi-natural habitats modulate the effectiveness of flower-rich agri-environment schemes to promote pollinator visitation in crop fields', *Agriculture, Ecosystems & Environment*, 284, pp.1-8 (106590). DOI: 10.1016/j.agee.2019.106590.

Laliberte, A.S., Goforth, M.A., Steele, C.M. and Rango, A. (2011). 'Multispectral Remote Sensing from Unmanned Aircraft: Image Processing Workflows and Applications for Rangeland Environments', *Remote Sensing*, 3, pp. 2529-2551; DOI: 10.3390/rs3112529.

Landmann, T., Piiroinen, R., Makori, D.M., Abdel-Rahman, E.M., Makau, S., Pellikka, P. and Raina, S.K. (2015). 'Application of hyperspectral remote sensing for flower mapping in African savannas', *Remote Sensing of Environment*, 166, pp. 50-60. DOI: 10.1016/j.rse.2015.06.006.

Landmann, T., Feilhauer, H., Shen, M., Chen, J., Raina, S. (2018). Mapping the distribution and abundance of flowering plants using hyperspectral sensing. In: Thenkabail, P.S., Lyon, J.G. and Huete, A. eds. *Advanced Applications in Remote Sensing of Agricultural Crops and Natural Vegetation*. 2nd ed. CRC Press, pp. 69-78. DOI: 10.1201/9780429431166-4.

Langlois, A., Jacquemart, A-L. and Piqueray, J. (2020). 'Contribution of Extensive Farming Practices to the Supply of Floral Resources for Pollinators', *Insects*, 11(818), pp. 1-19. DOI: 10.3390/insects11110818.

Lary, D.J.; Alavi, A.H.; Gandomi, A.H. and Walker, A.L. (2016). 'Machine learning in geosciences and remote sensing', *Geoscience Frontiers*, 7 (1), pp. 3-10. DOI: 10.1016/j.gsf.2015.07.003.

Latty, R.S., Nelson, R., Markham, B., Williams, D., Toll, D. and Irons, J. (1985). 'Performance Comparisons Between Information Extraction Techniques Using Variable Spatial Resolution Data', *Photogrammetric Engineering and Remote Sensing*, 51 (9), pp. 1459-1470. DOI: 0099-1112/85/5109-1459$02.25/0.

Le Féon, V., Burel, F., Chifflet, R., Henry, M., Ricroch, A., Vaissière, B.E. and Baudry, J. (2013). 'Solitary bee abundance and species richness in dynamic agricultural landscapes', *Agriculture, Ecosystems and Environment*, 166, pp. 94-101. DOI: 10.1016/j.agee.2011.06.020.

LeBuhn, G. and Vargas Luna, J. (2021). 'Pollinator decline: what do we know about the drivers of solitary bee declines?', *Current Opinion in Insect Science*, 46, pp. 106–111. DOI: 10.1016/j.cois.2021.05.004.

Lecocq, A., Kryger, P., Vejsnæs, F. and Jensen, A.B. (2015) 'Weight Watching and the Effect of Landscape on Honeybee Colony Productivity: Investigating the Value of Colony Weight Monitoring for the Beekeeping Industry', *PLoS ONE*, 10(7), pp. 1-14 (e0132473). DOI: 10.1371/journal.pone.0132473.

Lefsky, M.A., Cohen, W.B., Parker, G.G. and Harding, D.J. (2002). 'Lidar Remote Sensing for Ecosystem Studies: Lidar, an emerging remote sensing technology that directly measures the three-dimensional distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of particular interest to forest, landscape, and global ecologists', *BioScience*, 52(1), pp. 19–30. DOI: 10.1641/0006-3568(2002)052[0019:LRSFES]2.0.CO;2.

Leong, M. and Roderick, G.K. (2015). 'Remote sensing captures varying temporal patterns of vegetation between human-altered and natural landscapes', *PeerJ*, 3, pp. 1-17 (e1141). DOI: 10.7717/peerj.1141.

Leonhardt, S.D. and Blüthgen, N. (2012). 'The same, but different: pollen foraging in honeybee and bumblebee colonies', *Apidologie*, 43, pp. 449–464. DOI: 10.1007/s13592-011-0112-y.

Leutner, B., Horning, N. and Schwalb-Willmann, J. (2019). *RStoolbox: Tools for remote sensing data analysis.* Version 0.2.6. [R package]. URL: <https://CRAN.R-project.org/package=RStoolbox>.

Lillesand, T.M., Kiefer, R.W. and Chipman, J.W. (2015). *Remote Sensing and Image Interpretation*. 7th ed. Hoboken: Wiley.

Limagrain. (2021) 'Our Products' <URL: https://www.lgseeds.co.uk/crops/> [Accessed: 31/12/2021].

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N. and Greenleaf, S. (2009). 'Modelling pollination services across agricultural landscapes', *Annals of Botany*, 103 (9), pp. 1589–1600. DOI: 10.1093/aob/mcp069.

Lowe, E.B., Groves, R. and Gratton, C. (2021). 'Impacts of field-edge flower plantings on pollinator conservation and ecosystem service delivery – A meta-analysis', *Agriculture, Ecosystems & Environment*, 310, 107290, pp. 1-10, DOI: 10.1016/j.agee.2020.107290.

Lu, D. and Weng, Q. (2007). 'A survey of image classification methods and techniques for improving classification performance', *International Journal of Remote Sensing*, 28 (5), pp. 823–870. DOI: 10.1080/01431160600746456

Luoto, M., Kuussaari, M. and Toivonen, T. (2002) 'Modelling Butterfly Distribution Based on Remote Sensing Data', *Journal of Biogeography*, 29 (8), pp. 1027-1037. DOI: 10.1046/j.1365-2699.2002.00728.x.

Lye, G.C., Osborne, J.L. Park, K.J. and Goulson, D. (2012). 'Using citizen science to monitor *Bombus* populations in the UK: nesting ecology and relative abundance in the urban environment', *Journal of Insect Conservation*, 16, pp. 697–707. DOI: 10.1007/s10841-011-9450-3.

Maher, S., Manco, F. and Ings, T.C. (2019). 'Using citizen science to examine the nesting ecology of ground-nesting bees', *Ecosphere*, 10(10), pp. 1-13, e02911. DOI: 10.1002/ecs2.2911.

Mallinger, R.E., Gibbs, J. and Gratton, C. (2016). 'Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods', *Landscape Ecology*, 31, pp. 1523–1535. DOI: 10.1007/s10980-015-0332-z.

Mansour, K. Mutanga, O., Adam, E. and Abdel-Rahman, E.M. (2016). 'Multispectral remote sensing for mapping grassland degradation using the key indicators of grass species and edaphic factors', *Geocarto International*, 31(5), pp. 477-491, DOI: 10.1080/10106049.2015.1059898

Martin, E.A. et al. (2019). 'The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe', *Ecology Letters*, 22, pp. 1083–1094. DOI: 10.1111/ele.13265.

Martins, A.C., Gonçalves, R.B., Melo, G.A.R. (2013). 'Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years', *ZOOLOGIA*, 30(2), pp.157–176. DOI: 10.1590/S1984-46702013000200006.Melin, M., Shapiro, A.C. and Glover-Kapfer, P. (2017). *LiDAR for ecology and conservation*. WWF Conservation Technology Series 1(3). Woking, United Kingdom: WWF-UK. DOI: 10.13140/RG.2.2.22352.76801.

Matongera, T.N., Mutanga, O., Dube, T. and Sibanda, M. (2017). 'Detection and mapping the spatial distribution of bracken fern weeds using the Landsat 8 OLI new generation sensor', *International Journal of Applied Earth Observation and Geoinformation*, 57, pp. 93-103. DOI: 10.1016/j.jag.2016.12.006. Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. and Nowakowski, M. (2002). 'The effect of arable field margin composition on invertebrate biodiversity', *Biological Conservation*, 106 (2), pp.259-271. DOI: 10.1016/S0006-3207(01)00252-X.

Meikle, W.G., Rector, B.G., Mercadier, G. and Holst, N. (2008). 'Within-day variation in continuous hive weight data as a measure of honey bee colony activity', *Apidologie,* 39(6). Pp. 694- 707. DOI: 10.1051/apido:2008055.

Michelot-Antalik, A., Michel, N., Goulnik, J., Blanchetête, A., Delacroix, E., Faivre-Rampant, P., Fiorelli, J-L., Galliot, J-N., Genoud, D., Lanore, L., Le Clainche, I., Le Paslier, M.C., Novak, S., Odoux, J-F., Brunel, D. and Farruggia, A. (2021). 'Comparison of grassland plant-pollinator networks on dairy farms in three contrasting French landscapes', *Acta Oecologica*, 112, pp. 103763, DOI: 10.1016/j.actao.2021.103763.

Michez, A., Piégay, H., Jonathan, L., Claessens, H. and Lejeune, P. (2016). 'Mapping of riparian invasive species with supervised classification of Unmanned Aerial System (UAS) imagery', *International Journal of Applied Earth Observation and Geoinformation*, 44, pp. 88-94. DOI: 10.1016/j.jag.2015.06.014.

Microsoft. (2021a). 'RANDBETWEEN function', URL: <https://support.microsoft.com/en-us/office/randbetween-function-4cc7f0d1-87dc-4eb7-987f-a469ab381685> [Accessed: 12/10/2021].

Microsoft. (2021b). 'RAND function', URL: <https://support.microsoft.com/en-us/office/rand-function-4cbfa695-8869-4788-8d90-021ea9f5be73> [Accessed: 12/10/2021].

Middleton, E.G., MacRae, I.V. and Philips, C.R. (2021). 'Floral Plantings in Large-Scale Commercial Agroecosystems Support Both Pollinators and Arthropod Predators', *Insects*, 12(2), pp. 1-18 (91). DOI: 10.3390/insects12020091.

Millard, J.W., Freeman, R. and Newbold, T. (2020). 'Text-analysis reveals taxonomic and geographic disparities in animal pollination literature', *Ecography*, 43(1), pp.44-59. DOI: 10.1111/ecog.04532.

Minařík, R., Langhammer, J. and Hanuš, J. (2019). 'Radiometric and Atmospheric Corrections of Multispectral μMCA Camera for UAV Spectroscopy', *Remote Sensing*, 11(20), pp. 1-31 (2428). DOI: 10.3390/rs11202428.

Moerman, R., Vanderplanck, M., Fournier, D., Jacquemart, A-L. and Michez, D. (2017). 'Pollen nutrients better explain bumblebee colony development than pollen diversity', *Insect Conservation and Diversity*, 10, pp. 171–179. DOI: 10.1111/icad.12213.

Morandin, L.A., Long, R.F. and Kremen, C. (2014). 'Hedgerows enhance beneficial insects on adjacent tomato fields in an intensive agricultural landscape', *Agriculture, Ecosystems and Environment*, 189, pp. 164–170. DOI: 10.1016/j.agee.2014.03.030.

Morton, R. D., Marston, C. G., O'Neil, A. W., Rowland, C. S. (2020). *Land Cover Map 2019 (land parcels, GB)*. NERC Environmental Information Data Centre. DOI: 10.5285/44c23778-4a73-4a8f-875f-89b23b91ecf8.

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C. and Dorn, S. (2006). 'Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee–flower relationships', *Biological Conservation*, 130(4), pp. 604-615. DOI: 10.1016/j.biocon.2006.01.023.

Müllerová, J., Bartaloš, T., Brůna, J., Dvořák, P. and Vítková, M. (2017a). 'Unmanned aircraft in nature conservation – an example from plant invasions', *International Journal of Remote Sensing*, 38 (8-10), pp. 2177-2198. DOI: 10.1080/01431161.2016.1275059.

Müllerová, J., Brůna, J., Bartaloš, T., Dvořák, P., Vítková, M. and Pyšek, P. (2017b). 'Timing Is Important: Unmanned Aircraft vs. Satellite Imagery in Plant Invasion Monitoring', *Frontiers in Plant Science*, 8(887), pp. 1-13. DOI: 10.3389/fpls.2017.00887.

NASA. (2021). 'Airborne Visible / Infrared Imaging Spectrometer', URL: <https://aviris.jpl.nasa.gov/> [Accessed: 30/09/2021].

NatureGate. (2020). '*Plants*', URL: <http://www.luontoportti.com/suomi/en/kasvit/> [Accessed: 07/12/2020].

Nepi, M. (2014). ‘Beyond nectar sweetness: the hidden ecological role of non-protein amino acids in nectar’, *Journal of Ecology*, 102(1), pp. 108-115. DOI: 10.1111/1365-2745.12170.

Neumann, C., Behling, R., Schindhelm, A., Itzerott, S., Weiss, G., Wichmann, M. and Müller, J. (2020). ‘The colors of heath flowering - quantifying spatial patterns of phenology in Calluna life-cycle phases using high-resolution drone imagery’, *Remote Sensing in Ecology and Conservation*, 6(1), pp. 35-51. DOI: 10.1002/rse2.121.

Neumüller, U., Burger, H., Krausch, S., Blüthgen, N. and Ayasse, M. (2020). ‘Interactions of local habitat type, landscape composition and flower availability moderate wild bee communities’, *Landscape Ecology*, 35, pp. 2209–2224. DOI: 10.1007/s10980-020-01096-4.

Nichols, R.N., Goulson, D. and Holland, J.M. (2019). ‘The best wildflowers for wild bees’, *Journal of Insect Conservation*, 23, pp. 819–830. DOI: 10.1007/s10841-019-00180-8.

Nicholson, C.C., Ricketts, T.H., Koh, I., Smith, H.G., Lonsdorf, E.V. and Olsson, O. (2019). ‘Flowering resources distract pollinators from crops: Model predictions from landscape simulations’, *Journal of Applied Ecology*, 56(3), pp. 618-628. DOI: 10.1111/1365-2664.13333.

Nicholson, C.C., Ward, K.L., Williams, N.M., Isaacs, R., Mason, K.S., Wilson, J.K., Brokaw, J., Gut, L.J., Rothwell, N.L., Wood, T.J., Rao, S., Hoffman, G.D., Gibbs, J., Thorp, R.W. and Ricketts, T.H. (2020). ‘Mismatched outcomes for biodiversity and ecosystem services: testing the responses of crop pollinators and wild bee biodiversity to habitat enhancement’, *Ecology Letters*, 23, pp. 326–335. DOI: 10.1111/ele.13435.

Nicolson, S.W. (2011). ‘Bee Food: The Chemistry and Nutritional Value of Nectar, Pollen and Mixtures of the Two’, *African Zoology*, 46(2), pp. 197-204. DOI: 10.3377/004.046.0201.

Nitze, I., Schulthess, U. and Asche, H. (2012). ‘Comparison of Machine Learning Algorithms Random Forest, Artificial Neural Network and Support Vector Machine to Maximum Likelihood for Supervised Crop Type Classification’, In: Feitosa, R.Q., da Costa, G.A.O.P., de Almeida, C.M., Fonseca, L.M.G. and Kux, H.J.H. eds. *Proceedings of the 4th GEOBIA, 7-9 May, Rio de Janeiro, Brazil*. Brazilian National Institute for Space Research (INPE), pp. 35-40.

Norasma, C.Y.N., Fadzilah, M.A., Roslin, N.A., Zanariah, Z.W.N., Tarmidi, Z. and Candra, F.S. (2019). ‘Unmanned Aerial Vehicle Applications In Agriculture’, *IOP Conference Series: Materials Science and Engineering*, 506, pp. 1-10 (012063). DOI: 10.1088/1757-899X/506/1/012063.

Nowakowski, M and Pywell, R. (2016). ‘Habitat Creation and Management for Pollinators’, *Centre for Ecology and Hydrology*, Wallingford, UK.

O'Brien, C. and Arathi, H.S. (2021). 'If You Build It, They Will Come—Agroecosystem-Based Management Practices Support Pollinators', *Annals of the Entomological Society of America*, 114(3), pp. 322-328. DOI: 10.1093/aesa/saaa037.

Ogilvie, J.E. and Forrest, J.R.K. (2017). 'Interactions between bee foraging and floral resource phenology shape bee populations and communities', *Current Opinion in Insect Science*, (21), pp. 75-82. DOI: 10.1016/j.cois.2017.05.015.

Ollerton, J., Winfree, R., and Tarrant, S. (2011). 'How many flowering plants are pollinated by animals?', *OIKOS*, 120(3), pp. 321-326. DOI: 10.1111/j.1600-0706.2010.18644.x.

Ollerton, J., Erenler, H., Edwards, M. and Crockett, R. (2014). 'Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes', *Science*, 346 (6215), pp. 1360-1362. DOI: 10.1126/science.1257259.

Ollerton, J. (2017). 'Pollinator Diversity: Distribution, Ecological Function, and Conservation', *Annual Review of Ecology, Evolution and Systematics*, 48(1), pp. 353-376. DOI: 10.1146/annurev-ecolsys-110316-022919.

Olofsson, P., Foody, G.M., Stehman, S.V. and Woodcock, C.E. (2013). 'Making better use of accuracy data in land change studies: Estimating accuracy and area and quantifying uncertainty using stratified estimation', *Remote Sensing of Environment*, 129, pp. 122-131. DOI: 10.1016/j.rse.2012.10.031.

Olsson, O. and Bolin, A. (2014). 'A model for habitat selection and species distribution derived from central place foraging theory', *Oecologia*, 175(2), pp. 537-548. DOI: 10.1007/s00442-014-2931-9.

Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J. and Sanderson, R.A. (2008). 'Quantifying and comparing bumblebee nest densities in gardens and countryside habitats', *Journal of Applied Ecology*, 45(3), pp. 784-792. DOI: 10.1111/j.1365-2664.2007.01359.x.

Ouvrard, P., Transon, J. and Jacquemart, A-L. (2018). 'Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects', *Biodiversity and Conservation*, 27, pp. 2193–2216. DOI: 10.1007/s10531-018-1531-0.

Ouvrard, P. and Jacquemart, A-L. (2018b). 'Agri-environment schemes targeting farmland bird populations also provide food for pollinating insects', *Agricultural and Forest Entomology*, 20(4), pp. 558-574. DOI: 10.1111/afe.12289.

Ovenden, G.N., Swash, A.R.H. and Smallshire, D. (1998) ‘Agri-Environment Schemes and their Contribution to the Conservation of Biodiversity in England’, *Journal of Applied Ecology*, 35(6), pp. 955-960.

Pamminger, T., Becker, R., Himmelreich, S., Schneider, C.W. and Bergtold, M. (2019). ‘The nectar report: quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural and non-agricultural landscapes’, *PeerJ*, 7, pp. 1-15 (e6329). DOI 10.7717/peerj.6329.

Peña-Barragán, J.M., López-Granados, F., Jurado-Expósito, M. and García-Torres, L. (2007). ‘Mapping *Ridolfia segetum* patches in sunflower crop using remote sensing’, *Weed Research*, 47(2), pp. 164-172. DOI: 10.1111/j.1365-3180.2007.00553.x.

Pettorelli, N., Schulte toBühne, H., Shapiro, A.C. and Glover-Kapfer, P. (2018a). *Satellite Remote Sensing for Conservation*. WWF Conservation Technology Series 1(4). WWF. DOI: 10.13140/RG.2.2.25962.41926.

Pettorelli, N., Schulte to Bühne, H., Tulloch, A., Dubois, G., Macinnis-Ng, C., Queirós, A.M., Keith, D.A., Wegmann, M., Schrodt, F., Stellmes, M., Sonnenschein, R., Geller, G.N., Roy, S., Somers, B., Murray, N., Bland, L., Geijzendorffer, I., Kerr, J.T., Broszeit, S., Leitão, P.J., Duncan, C., El Serafy, G., He, K.S., Blanchard, J.L., Lucas, R., Mairota, P., Webb, T.J. and E. Nicholson (2018b). ‘Satellite remote sensing of ecosystem functions: opportunities, challenges and way forward’, *Remote Sensing in Ecology and Conservation*, 4 (2), pp. 71–93. DOI: 10.1002/rse2.59.

Pitsford School. (2021). ‘Pitsford weather’, URL: http://www.northantsweather.org/ [Accessed: 09/12/2021].

Planet Labs. (2021). ‘Planet Platform’ URL: <https://www.planet.com/products/platform/> [Accessed: 22/12/2022]

Pollard, E. and Yates, T.J. (1993). *Monitoring Butterflies for Ecology and Conservation.* London: Chapman & Hall.

Potapov P.V., Turubanova S.V., Hansen , M.C., Adusei, B., Broich, M., Altstatt, A., Mane, L. and Justice, C.O. (2012). ‘Quantifying forest cover loss in Democratic Republic of the Congo, 2000-2010, with Landsat ETM+ data', *Remote Sensing of Environment*, 122 (Landsat Legacy Special Issue), pp. 106-116. DOI: 10.1016/j.rse.2011.08.027

Pottier, J., Malenovský, Z., Psomas, A., Homolová, L., Schaepman, M.E., Choler, P., Thuiller, W., Guisan, A. and Zimmermann, N.E. (2014). ‘Modelling plant species distribution in alpine grasslands using airborne imaging spectroscopy', *Biology Letters*, 10 (7), pp. 1-4. DOI: 10.1098/rsbl.2014.0347.

Potts, S.G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G. and Twillmer, P.A. (2005). 'Role of nesting resources in organising diverse bee communities in a Mediterranean landscape', *Ecological Entomology*, 30, pp. 78-85. DOI: 10.1111/j.0307-6946.2005.00662.x.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W.E. (2010). 'Global pollinator declines: trends, impacts and drivers', *Trends in Ecology and Evolution*, 25 (6), pp. 345-353. DOI: 10.1016/j.tree.2010.01.007.

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J. and Vanbergen, A.J. (2016). 'Safeguarding pollinators and their values to human well-being', *Nature*, 540, pp. 220-229. DOI: 10.1038/nature20588.

Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A. and Isaac, N.J.B. (2019). 'Widespread losses of pollinating insects in Britain', *Nature Communications*, 10 (1018), pp. 1-6. DOI: 10.1038/s41467-019-08974-9.

Pu, R., Landry, S. and Yu, Q. (2011). 'Object-based urban detailed land cover classification with high spatial resolution IKONOS imagery', *International Journal of Remote Sensing*, 32 (12), pp.3285-3308. DOI: 10.1080/01431161003745657.

Purvis, E.E.N., Meehan, M.L. and Lindo, Z. (2020). 'Agricultural field margins provide food and nesting resources to bumble bees (*Bombus* spp., Hymenoptera: Apidae) in Southwestern Ontario, Canada', 13(3), *Insect Conservation and Diversity*, 219-228. DOI: 10.1111/icad.12381.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. and Sherwood, A. (2005). 'Providing foraging resources for bumblebees in intensively farmed landscapes', *Biological Conservation*, 121 (4), pp. 479-494. DOI: 10.1016/j.biocon.2004.05.020.

Pywell, R.F., Meek, W.R., Hulmes, L., Hulmes, S., James, K.L., Nowakowski, M. and Carvell, C. (2011). 'Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes', *Journal of Insect Conservation*, 15, pp. 853–864. DOI: 10.1007/s10841-011-9383-x.

Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M. and Bullock, J.M. (2015) 'Wildlife-friendly farming increases crop yield: evidence for ecological intensification', *Proceedings of the Royal Society B*, 282 (1816), pp. 20151740. DOI: 10.1098/rspb.2015.1740.

QGIS (2020). *QGIS Geographic Information System*. Version 3.4.15-Madeira [computer program]. Open Source Geospatial Foundation Project.

Raab, C., Riesch, F., Tonn, B., Barrett, B., Meißner, M., Balkenhol, N. and Isselstein, J. (2020). ‘Target-oriented habitat and wildlife management: estimating forage quantity and quality of semi-natural grasslands with Sentinel-1 and Sentinel-2 data’, *Remote Sensing in Ecology and Conservation*, 6 (3 - Special Issue: Ecoacoustics and Biodiversity Monitoring), pp. 381-398. DOI: 10.1002/rse2.149

Rands, S.A. and Whitney, H.M. (2011). ‘Field Margins, Foraging Distances and Their Impacts on Nesting Pollinator Success’, *PLoS ONE*, 6(10), pp.1-8 (e25971). DOI: 10.1371/journal.pone.0025971

Reverté, S., Retana, J., Gómez, J.M. and Bosch, J. (2016). ‘Pollinators show flower colour preferences but flowers with similar colours do not attract similar pollinators’, *Annals of Botany*, 118(2), pp. 249–257. DOI: 10.1093/aob/mcw103.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng’, A., Potts, S.G. and Viana, B.F. (2008). ‘Landscape effects on crop pollination services: are there general patterns?’, *Ecology Letters*, 11 (5), pp. 499-515. DOI: 10.1111/j.1461-0248.2008.01157.x.

Robinson, R.A. and Sutherland, W.J. (2002). ‘Post-war changes in arable farming and biodiversity in Great Britain’, *Journal of Applied Ecology*, 39 (1), pp. 157-176. DOI: 10.1046/j.1365-2664.2002.00695.x.

Rodger, J.G., Bennett, J.M., Razanajatovo, M., Knight, T.M., Van Kleunen, M. Ashman, T-L., Steets, J.A., Hui, C., Arceo-Gómez, G., Burd, M., Burkle, L.A., Burns, J.H., Durka, W., Freitas, L., Kemp, J.E., Li, J., Pauw, A., Vamosi, J.C., Wolowski, M., Xia, J. and Ellis, A.G. (2021). ‘Widespread vulnerability of flowering plant seed production to pollinator declines’, *Science Advances*, 7(42), DOI: 10.1126/sciadv.abd3524.

Rose, D.C., Sutherland, W.J., Parker, C., Lobley, M., Winter, M., Morris, C., Twining, S., Ffoulkes, C., Amano, T. and Dicks, L.V. (2016) ‘Decision support tools for agriculture: Towards effective design and delivery’, *Agricultural Systems*, 149, pp. 165-174.

Rotheray, E. L., Osborne, J. L., and Goulson, D. (2017). ‘Quantifying the food requirements and effects of food stress on bumble bee colony development’, *Journal of Apicultural Research*, 56, pp. 288–299. DOI: 10.1080/00218839.2017.130771.

Roulston, T.H., Cane, J.H., and Buchmann, S.L. (2000) ‘What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny?’, *Ecological Monographs*, 70 (4), pp. 617-643.

Roulston, T.H. and Cane, J.H. (2002) ‘The effect of pollen protein concentration on body size in the sweat bee Lasioglossum zephyrum (Hymenoptera: Apiformes)’, Evolutionary Ecology, 16, pp. 49-65. DOI: 10.1023/A:1016048526475

Roulston, T.H. and Goodell, K. (2011). ‘The Role of Resources and Risks in Regulating Wild Bee Populations’, *Annual Review of Entomology*, 56, pp. 293–312. DOI: 10.1146/annurev-ento-120709-144802.

R. (2021). *R X 64*. Version 4.0.5 [Computer program].

RTKLIB (2013). *RTKLIB: An Open Source Program Package for GNSS Positioning*. Version 2.4.2 [computer program].

Ruedenauer, F.A., Raubenheimer, D., Kessner-Beierlein, D., Grund-Mueller, N., Noack, L., Spaethe, J. and Leonhardt, S.D. (2020). ‘Best be(e) on low fat: linking nutrient perception, regulation and fitness’, *Ecology Letters*, 23, pp. 545–554. DOI: 10.1111/ele.13454.

Russo, L., Vaudo, A.D., Fisher, C.J., Grozinger, C.M. and Shea, K. (2019). ‘Bee community preference for an invasive thistle associated with higher pollen protein content’, *Oecologia*, 190, pp.901–912. DOI: 10.1007/s00442-019-04462-5.

Ruwaimana, M., Satyanarayana, B., Otero, V. M., Muslim, A., Syafiq, A. M., Ibrahim, S., Raymaekers, D., Koedam, N. and Dahdouh-Guebas, F. (2018). ‘The advantages of using drones over space-borne imagery in the mapping of mangrove forests’, *PLoS ONE,* 13(7), pp. e0200288. DOI: 10.1371/journal.pone.0200288.

Sankey, T.T., McVay, J., Swetnam, T.L., McClaran, M.P., Heilman, P. and Nichols, M. (2018). ‘UAV hyperspectral and lidar data and their fusion for arid and semi-arid land vegetation monitoring’, *Remote Sensing in Ecology and Conservation*, 4 (1), pp. 20–33. DOI: 10.1002/rse2.44.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G. and Kleijn, D. (2013). ‘Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis’, *Ecology Letters*, 16 (7), pp. 912–920. DOI: 10.1111/ele.12128.

Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T.J., Schaminée, J.H.J., Siepel, H. and Kleijn, D. (2014). ‘Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands.', *PNAS*, 111(49), pp. 17552-17557. DOI: 10.1073/pnas.1412973111.

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J. and Kleijn, D. (2015). 'Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries', *Journal of Applied Ecology*, 52(5), pp. 1165-1175. DOI: 10.1111/1365-2664.12479.

Schmid, T., Koch, M., Gumuzzio, J. and Mather, P.M. (2004). 'A spectral library for a semi-arid wetland and its application to studies of wetland degradation using hyperspectral and multispectral data', *International Journal of Remote Sensing*, 25(13), pp. 2485-2496. DOI: 10.1080/0143116031000117001.

Schmidt, J., Fassnacht, F.E., Förster, M. and Schmidtlein, S. (2018). 'Synergetic use of Sentinel-1 and Sentinel-2 for assessments of heathland conservation status', *Remote Sensing in Ecology and Conservation*, 4 (3), pp. 225–239. DOI: 10.1002/rse2.68.

Seeley, T.D., Camazine, S. and Sneyd, J. (1991). 'Collective decision-making in honey bees: how colonies choose among nectar sources', *Behavioral Ecology and Sociobiology*, 28(4), pp. 277-290. DOI: 10.1007/BF00175101.

Senapathi, D., Fründ, J., Albrecht, M., Garratt, M.P.D., Kleijn, D., Pickles, B.J., Potts, S.G., An, J., Andersson, G.K.S., Bänsch, S., Basu, P., Benjamin, F., Bezerra, A.D.M., Bhattacharya, R., Biesmeijer, J.C., Blaauw, B., Blitzer, E.J., Brittain, C.A., Carvalheiro, L.G., Cariveau, D.P., Chakraborty, P., Chatterjee, A., Chatterjee, S., Cusser, S., Danforth, B.N., Degani, E., Freitas, B.M., Garibaldi, L.A., Geslin, B., de Groot, G.A., Harrison, T., Howlett, B., Isaacs, R., Jha, S., Klatt, B.K., Krewenka, K., Leigh, S., Lindström, S.A.M., Mandelik, Y., McKerchar, M., Park, M., Pisanty, G., Rader, R., Reemer, M., Rundlöf, M., Smith, B., Smith, H.G., Silva, P.N., Steffan-Dewenter, I., Tscharntke, T., Webber, S., Westbury, D.B., Westphal, C., Wickens, J.B., Wickens, V.J., Winfree, R., Zhang, H. and Klein, A.-M. (2021). 'Wild insect diversity increases inter-annual stability in global crop pollinator communities', *Proceedings of the Royal Society B*, 288 (1947), pp.1-10 (20210212). DOI: 10.1098/rspb.2021.0212.

Senf, C., Leitão, P.J., Pflugmacher, D., van der Linden, S. and Hostert, P. (2015). 'Mapping land cover in complex Mediterranean landscapes using Landsat: Improved classification accuracies from integrating multi-seasonal and synthetic imagery', *Remote Sensing of Environment*, 156, pp. 527-536. DOI: 10.1016/j.rse.2014.10.018.

Shanmugam, P., Ahn, Y-H. and Sanjeevi, S. (2006). ‘A comparison of the classification of wetland characteristics by linear spectral mixture modelling and traditional hard classifiers on multispectral remotely sensed imagery in southern India’, *Ecological Modelling*, 194 (4), pp. 379–394. DOI: 10.1016/j.ecolmodel.2005.10.033.

Shepherd, K.D. and Walsh, M.G. (2002). ‘Development of Reflectance Spectral Libraries for Characterization of Soil Properties’, *Soil Science Society of America Journal*, 66, pp. 988–998. DOI: 10.2136/sssaj2002.0988.

Sivinski, J., Wahl, D., Holler, T., Al Dobai, S. and Sivinski, R. (2011). ‘Conserving natural enemies with flowering plants: Estimating floral attractiveness to parasitic Hymenoptera and attraction’s relationship to flower and plant morphology’, *Biological Control*, 58(3), pp. 208-214. DOI: 10.1016/j.biocontrol.2011.05.002.

Siviter, H., Bailes, E.J., Martin, C.D., Oliver, T.R., Koricheva, J., Leadbeater E. and Brown, M.J.F. (2021). ‘Agrochemicals interact synergistically to increase bee mortality’, *Nature*, 596, pp. 389–392. DOI: 10.1038/s41586-021-03787-7.

Smessaert, J., Honnay, O. and Keulemans, W. (2019). ‘Monitoring pollinator activity in an apple and pear orchard, linked with the analysis of the nectar composition’, *Acta Horticulturae*, 1231, pp. 59-66. DOI: 10.17660/ActaHortic.2019.1231.11.

Smith, G.M. and Milton, E.J. (1999). ‘The use of the empirical line method to calibrate remotely sensed data to reflectance’, *International Journal of Remote Sensing*, 20(13), pp. 2653-2662. DOI: 10.1080/014311699211994.

Smith, C. and Warren, M. (2019). *GLMs in R for Ecology*. Great Britain: Smith and Warren.

Soroye, P., Newbold, T. and Kerr, J. (2020). ‘Climate change contributes to widespread declines among bumble bees across continents’, *Science*, 367, pp. 685-688. DOI: 10.1126/science.aax8591.

Stace, C.A. (2010). *New Flora of the British Isles*. 3rd ed. Cambridge, UK: Cambridge University Press.

Staley, J.T., Sparks, T.H., Croxton, P.J., Baldock, K.C.R., Heard, M.S., Hulmes, S., Hulmes, L., Peyton, J., Amy, S.R. and Pywell, R.F. (2012). ‘Long-term effects of hedgerow management policies on resource provision for wildlife’. *Biological Conservation*, 145 (1), pp. 24–29. DOI: 10.1016/j.biocon.2011.09.006.

Stang, M., Klinkhamer, P.G.L. and Van Der Meijden, E. (2006). ‘Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web’, *OIKOS*, 112(1), pp. 111-121. DOI: 10.1111/j.0030-1299.2006.14199.x.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., and Tscharntke. T. (2002) ‘Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds’, *Ecology*, 83 (5), pp. 1421-1432.

Story, M. and Congalton, R.G. (1986). ‘Accuracy Assessment: A User's Perspective’, *Photogrammetric Engineering and Remote Sensing*, 52 (3), pp. 397-399. DOI: 0099-1112/86/5203-397$02.25/0.

Streck, N.A., Rundquist, D. and Connot, J. (2003). ‘Spectral signature of selected soils’, *Revista Brasileira de Agrometeorologia*, 11 (1), pp. 181-184.

Sulborska, A. and Weryszko-Chmielewska, E.(2006). ‘Morphology, anatomy and ultrastructure of yarrow (*Achillea millefolium* L.) floral nectaries’, *Acta Agrobotanica*, 59(1), pp. 17-28. DOI: 10.5586/aa.2006.002

Szigeti, V., Korösi, A., Harnos, A., Nagy, J. and Kis, J. (2016). ‘Measuring floral resource availability for insect pollinators in temperate grasslands – a review’, *Ecological Entomology*, 41, pp. 231–240. DOI: 10.1111/een.12298.

Tansey, K., Chambers, I., Anstee, A., Denniss, A. and Lamb, A. (2009). ‘Object-oriented classification of very high resolution airborne imagery for the extraction of hedgerows and field margin cover in agricultural areas’, *Applied Geography*, 29 (2), pp.145-157. DOI: 10.1016/j.apgeog.2008.08.004.

Tasei, J-N. and Aupinel, P. (2008) ‘Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae)’, *Apidologie*, 39, pp. 397–409.

Tenkorang, F. and Lowenberg-DoBoer, J. (2008). ‘On-Farm Profitability of Remote Sensing in Agriculture’, *The Journal of Terrestrial Observation*, 1(1), pp. 50-59. DOI:

Tew, N.E., Memmott, J., Vaughan, I.P., Bird, S., Stone, G.N., Potts, S.G., Baldock, K.C.R. (2021). ‘Quantifying nectar production by flowering plants in urban and rural landscapes’, *Journal of Ecology*, 109(4), pp. 1747-1757. DOI: 10.1111/1365-2745.13598.

Timberlake, T.P., Vaughan, I.P. and Memmott, J. (2019). 'Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees', *Journal of Applied Ecology*, 56 (7), pp. 1585-1596. DOI: 10.1111/1365-2664.13403.

Timberlake, T.P., Vaughan, I.P., Baude, M. and Memmott, J. (2021). 'Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover', *Journal of Applied Ecology*, 00, pp. 1-11. DOI: 10.1111/1365-2664.13826.

Toll, D.L. (1985). 'Effect of Landsat Thematic Mapper Sensor Parameters on Land Cover Classification', *Remote Sensing of Environment*, 17 (2), pp. 129-140. DOI: 10.1016/0034-4257(85)90069-0.

Tonietto, R.K. and Larkin, D.J. (2018). 'Habitat restoration benefits wild bees: A meta-analysis', *Journal of Applied Ecology*, 55(2), pp. 582-590. DOI: 10.1111/1365-2664.13012.

Topcon. (2020). *HIPER V*, URL: <https://www.topconpositioning.com/support/products/hiper-v> [Accessed: 01/12/2020].

Trunschke, J., Lunau, K., Pyke, G.H., Ren, Z-X. and Wang, H. (2021). 'Flower Color Evolution and the Evidence of Pollinator-Mediated Selection', *Frontiers in Plant Science*, 12, pp. 1-20. article 617851. DOI: 10.3389/fpls.2021.617851.

Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najar-Rodriguez, A.J. and Jacot, K. (2016). 'Tailored flower strips promote natural enemy biodiversity and pest control in potato crops', *Journal of Applied Ecology*, 53 (4), pp. 1169-1176. DOI: 10.1111/1365-2664.12653.

Twiston-Davies, G., Becher, M.A. and Osborne, J.L. (2021) 'BEE-STEWARD: A research and decision-support software for effective land management to promote bumblebee populations', *Methods in Ecology and Evolution*, 00, pp. 1-7. DOI: 10.1111/2041-210X.13673.

UK Government. (2021a). 'AB8: Flower-rich margins and plots', URL: <https://www.gov.uk/countryside-stewardship-grants/flower-rich-margins-and-plots-ab8> [Accessed: 13/10/2021].

UK Government. (2021b). 'AB1: Nectar flower mix', URL: <https://www.gov.uk/countryside-stewardship-grants/nectar-flower-mix-ab1> [Accessed: 13/10/2021].

UK Government. (2021c) 'Countryside Stewardship', URL: < https://www.gov.uk/government/collections/countryside-stewardship> [Accessed: 22/12/2021]

UKCEH. (2020). *The UKCEH Land Cover Maps for 2017, 2018 and 2019*. V1.5.1. UKCEH. URL: <https://www.ceh.ac.uk/sites/default/files/2021-11/lcm2017-2019product_documentation_v1_5_1.pdf> [Accessed: 10/11/2022].

UKCEH. (2021). 'Land Cover Map 2019', URL: < https://catalogue.ceh.ac.uk/documents/31f4887a-1691-4848-b07c-61cdc468ace7> [Accessed: 25/11/2021].

Ulian, T., Diazgranados, M., Pironon, S., Padulosi, S., Liu, U., Davies, L., Howes, M-J.R., Borrell, J.S., Ondo, I., Pérez-Escobar, O.A., Sharrock, S., Ryan, P., Hunter, D., Lee, M.A., Barstow, C., Łuczaj, L., Pieroni, A., Cámara-Leret, R., Noorani, A., Mba, C., Womdim, R.N., Muminjanov, H., Antonelli, A., Pritchard, H.W. and Mattana, E. (2020). 'Unlocking plant resources to support food security and promote sustainable agriculture', *Plants People Planet*, 2(5), pp. 421-445. DOI: 10.1002/ppp3.10145.

Underwood, E.C., Ustin, S.L. and Ramirez, C.M. (2007). 'A Comparison of Spatial and Spectral Image Resolution for Mapping Invasive Plants in Coastal California', *Environmental Management*, 39, pp. 63–83. DOI: 10.1007/s00267-005-0228-9.

Uno, Y., Prasher, S.O., Patel, R.M., Strachan, I.B., Pattey, E. and Karimi, Y. (2005). 'Development of field-scale soil organic matter content estimation models in Eastern Canada using airborne hyperspectral imagery', *Canadian Biosystems Engineering*, 47, pp. 1.9-1.14.

Ustin, S.L., Roberts, D.A., Gamon, J.A., Asner, G.P. and Green, R.O. (2004). 'Using Imaging Spectroscopy to Study Ecosystem Processes and Properties', *BioScience*, 54(6), pp. 523–534. DOI: 10.1641/0006-3568(2004)054[0523:UISTSE]2.0.CO;2.

Vanajith, V., Daniel, S.G., Rugma, S. and Dhanya, M. (2021). 'Monitoring Drought using Multispectral Remote Sensing – A Case Study', *IOP Conference Series: Materials Science and Engineering*, 1145, pp. 1-8 (012086). DOI: 10.1088/1757-899X/1145/1/012086.

Vanbergen, A.J. (2021). 'A cocktail of pressures imperils bees', *Nature*, 596, pp. 351-352. DOI: 10.1038/d41586-021-02079-4.

Vannier, C. and Hubert-Moy, L. (2008). 'Detection of Wooded Hedgerows in High Resolution Satellite Images using an Object-Oriented Method', *IEEE International Geoscience and Remote Sensing Symposium 2008*, Boston, MA, USA, 7-11 July 2008, IEEE. pp. 731-734. DOI: 10.1109/IGARSS.2008.4779826.

Vannier, C., Vasseur, C., Hubert-Moy, L and Baudry, J. (2011). ‘Multiscale ecological assessment of remote sensing images’, *Landscape Ecology*, 26 (8), pp. 1053-1069. DOI: 10.1007/s10980-011-9626-y.

Van der Kooi, C.J., Dyer, A.G., Kevan, P.G. and Lunau, K. (2019). ‘Functional significance of the optical properties of flowers for visual signalling’, *Annals of Botany*, 123 (2), pp. 263–276. DOI: 10.1093/aob/mcy119.

Van Rijn, P.C.J. and Wäckers, F.L. (2016). ‘Nectar accessibility determines fitness, flower choice and abundance of hoverflies that provide natural pest control’, *Journal of Applied Ecology*, 53 (3), pp. 925–933. DOI: 10.1111/1365-2664.12605.

Van Swaay, C.A.M., Dennis, E.B., Schmucki, R., Sevilleja, C., Balalaikins, M., Botham, M., Bourn, N., Brereton, T., Cancela, J.P., Carlisle, B., Chambers, P., Collins, S., Dopagne, C., Escobés, R., Feldmann, R., Fernández-García, J. M., Fontaine, B., Gracianteparaluceta, A., Harrower, C., Harpke, A., Heliölä, J., Komac, B., Kühn, E., Lang, A., Maes, D., Mestdagh, X., Middlebrook, I., Monasterio, Y., Munguira, M.L., Murray, T.E., Musche, M., Õunap, E., Paramo, F., Pettersson, L.B., Piqueray, J., Settele, J., Stefanescu, C., Švitra, G., Tiitsaar, A., Verovnik, R., Warren, M.S., Wynhoff, I. and Roy, D.B. (2019). ‘*The EU Butterfly Indicator for Grassland species: 1990-2017: Technical Report*’. Butterfly Conservation Europe & ABLE/eBMS (www.butterfly-monitoring.net).

Vasiliev, D. and Greenwood, S. (2021). ‘The role of climate change in pollinator decline across the Northern Hemisphere is underestimated’, *Science of The Total Environment*, 775, pp. 1-11 (145788). DOI: 10.1016/j.scitotenv.2021.145788.

Vaudo, A.D., Tooker, J.F., Grozinger, C.M. and Patch, H.M. (2015). ‘Bee nutrition and floral resource restoration’, *Current Opinion in Insect Science*, 10, pp. 133–141. DOI: 10.1016/j.cois.2015.05.008.

Vaudo, A. D., Patch, H.M., Mortensen, D.A., Tooker, J.F. and Grozinger, C.M. (2016) ‘Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences’, *Proceedings of the National Academy of Sciences of the United States of America*, 113 (28), pp. E4035–E4042. DOI: 10.1073/pnas.1606101113.

Vaudo, A.D., Tooker, J.F., Patch, H.M., Biddinger, D.J., Coccia, M., Crone, M.K., Fiely, M., Francis, J.S., Hines, H.M., Hodges, M., Jackson, S.W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E.D., Vanderplanck, M., Yip, E., Leonard, A.S. and Grozinger, C.M. (2020). ‘Pollen Protein: Lipid Macronutrient Ratios May Guide Broad Patterns of Bee Species Floral Preferences’, *insects*, 11(132), pp. 1-14. DOI: 10.3390/insects11020132.

Vickruck, J., Purvis, E.E.N., Kwafo, R., Kerstiens, H. and Galpern, P. (2021). ‘Diversifying Landscapes for Wild Bees: Strategies for North American Prairie Agroecosystems’, *Current Landscape Ecology Reports*, 6, pp. 85–96. DOI: 10.1007/s40823-021-00066-z.

Vignolini, S., Thomas, M.M., Kolle, M., Wenzel, T. Rowland, A., Rudall, P.J., Baumberg, J.J., Glover, B.J. and Steiner, U. (2012) ‘Directional scattering from the glossy flower of *Ranunculus*: how the buttercup lights up your chin’, *Journal of the Royal Society Interface*, 9(71), pp. 1295–1301. DOI: 10.1098/rsif.2011.0759.

Visscher, P.K. and Seeley, T.D. (1982). ‘Foraging Strategy of Honeybee Colonies in a Temperate Deciduous Forest’, *Ecology*, 63(6), pp. 1790-1801. DOI: 10.2307/1940121.Vray, S., Lecocq, T., Roberts, S.P.M. and Rasmont, P. (2017). ‘Endangered by laws: potential consequences of regulations against thistles on bumblebee conservation’, *Annales de la Societe Entomologique de France*, 53(1), pp.33-41. DOI: 10.1080/00379271.2017.1304831.

Walton, R.E., Sayer, C.D., Bennion, H. and Axmacher, J.C. (2020). ‘Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape’, *Biology Letters*, 16 (20190877), pp. 1-6. DOI: 10.1098/rsbl.2019.0877.

Wang, C., Myint, S., Price, K.P., Wang, H. and An, N. (2015). A simplified empirical line calibration method for sUAS-based remote sensing. In: *Imaging and Geospatial Technology Forum, IGTF 2015 - ASPRS Annual Conference and co-located JACIE Workshop*, 4-8 May 2015, Tampa, United States, American Society for Photogrammetry and Remote Sensing. pp.1-11.

Wardhaugh, C.W. (2015). ‘How many species of arthropods visit flowers?’, *Arthropod-Plant Interactions,* 9, pp. 547–565 (2015). DOI: 10.1007/s11829-015-9398-4.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., Van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D. and Ellis, S. (2021). ‘The decline of butterflies in Europe: Problems, significance, and possible solutions’, *PNAS*, 118(2), pp. 1-10 (e2002551117), DOI: 10.1073/pnas.2002551117.

Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. and Ollerton, J. (1996). ‘Generalization in Pollination Systems, and Why it Matters’, *Ecology*, 77(4), pp. 1043-1060. DOI: 10.2307/2265575.

Watkins and Doncaster. (2021). ‘Beginners butterfly net – complete’, URL: <https://www.watdon.co.uk/acatalog/E665-beginners-butterfly-net.html> [Accessed: 12/10/2021].

Weiner, C.N., Hilpert, A., Werner, M., Linsenmair, K.E., Blüthgen, N. (2010) 'Pollen amino acids and flower specialisation in solitary bees', *Apidologie*, 41, pp.476-487. DOI: 10.1051/apido/2009083.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Version 3.3.5. [R package]. New York: Springer-Verlag. URL: <https://ggplot2.tidyverse.org>.

Willcox, B.K., Robson, A.J., Howlett, B.G. and Rader, R. (2018). 'Toward an integrated approach to crop production and pollination ecology through the application of remote sensing', *PeerJ*, 6 (e5806); DOI:10.7717/peerj.5806.

Willmer, P. (2011) 'Rewards 2: The Biology of Nectar' In: Pollination and Floral Ecology. Princeton and Oxford: Princeton University Press.

Wix, N., Reich, M. and Schaarschmidt, F. (2019). 'Butterfly richness and abundance in flower strips and field margins: the role of local habitat quality and landscape context', *Heliyon*, 5(5), pp. 1-12. e01636. DOI: 10.1016/j.heliyon.2019.e01636.

Wood, T.J., Holland, J.M. and Goulson, D. (2017) 'Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species', *Journal of Applied Ecology*, 54 (1), pp. 323-333. DOI: 10.1111/1365-2664.12718.

Woodard, S.H., Federman, S., James, R.R., Danforth, B.N., Griswold, T.L., Inouye, D., McFrederick, Q.S., Morandin, L., Paul, D.L., Sellers, E., Strange, J.P., Vaughan, M., Williams, N.M., Branstetter, M.G., Burns, C.T., Cane, J., Cariveau, A.B., Cariveau, D.P., Childers, A., Childers, C., Cox-Foster, D.L., Evans, E.C., Graham, K.K., Hackett, K., Huntzinger, K.T., Irwing, R.E., Jha, S., Lawson, S., Liang, C., López-Uribe, M.M., Melathopoulos, A., Moylett, H.M.C., Otto, C.R.V., Ponisio, L.C., Richardson, L.L., Rose, R., Singh, R. and Wehling, W. (2020). 'Towards a U.S. national program for monitoring native bees', *Biological Conservation*, 252, pp. 1-6 (108821). DOI: 10.1016/j.biocon.2020.108821.

Woodard, S.H. and Jha, S. (2017) 'Wild bee nutritional ecology: predicting pollinator population dynamics, movement, and services from floral resources', *Current Opinion in Insect Science*, 21, pp. 83-90. DOI: 10.1016/j.cois.2017.05.011.

Woodcock, C.E. and Strahler, A.H. (1987). 'The Factor of Scale in Remote Sensing', *Remote Sensing of Environment*, 21 (3), pp. 311-332. DOI: 10.1016/0034-4257(87)90015-0.

Xavier, S.S., Coffin, A.W., Olson, D.M. and Schmidt, J.M. (2018). 'Remotely Estimating Beneficial Arthropod Populations: Implications of a Low-Cost Small Unmanned Aerial System' *Remote Sensing*, 10 (9), 1485. DOI:10.3390/rs10091485.

Xiang, T-Z., Xia, G-S. and Zhang, L. (2019). 'Mini-Unmanned Aerial Vehicle-Based Remote Sensing: Techniques, Applications, and Prospects', *IEEE Geoscience and Remote Sensing Magazine*, 7(3), pp. 29-63. DOI: 10.1109/MGRS.2019.2918840.

Xie, Z., Chen, Y., Lu, D., Li, G. and Chen, E. (2019). 'Classification of Land Cover, Forest, and Tree Species Classes with ZiYuan-3 Multispectral and Stereo Data', *Remote Sensing*, 11(2), pp. 1-27 (164). DOI: 10.3390/rs11020164.

Zacepins, A., Pecka, A., Osadcuks, V., Kviesis, A. and Engel, S. (2017) 'Solution for automated bee colony weight monitoring', *Agronomy Research*, 15(2), pp. 585–593.

Zamorano, J., Bartomeus, I., Grez, A.A. and Garibaldi, L.A. (2020). 'Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis', *Insect Conservation and Diversity*, 13(6), pp. 519-531. DOI: 10.1111/icad.12454.

Zhai, Z., Martínez, J.F., Beltran, V. and Martínez, N.L. (2020). 'Decision support systems for agriculture 4.0: Survey and challenges', *Computers and Electronics in Agriculture*, 170, pp. (105256). DOI: 10.1016/j.compag.2020.105256.

Zhang, J., Wang, C., Yuan, L., Liu, P., Zhang, Y. and Wu, K. (2020). 'Construction of a plant spectral library based on an optimised feature selection method', *Biosystems Engineering*, 195, pp. 1-16. DOI: 10.1016/j.biosystemseng.2020.04.008.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. and Dorn, S. (2010). 'Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances', *Biological Conservation*, 143, pp. 669–676. DOI: 10.1016/j.biocon.2009.12.003.

Appendices

Appendix 2.1 Species contained within the Emorsgate EM1 commercial mix grown within sown field margins

Latin name	Vernacular name
Achillea millefolium	Yarrow
Centaurea nigra	Common knapweed
Daucus Carota	Wild carrot
Galium verum	Lady's bedstraw
Leucanthemum vulgare	Oxeye daisy
Malva moschata	Musk mallow
Poterium sanguisorba	Salad burnet
Prunella vulgaris	Self-heal
Ranunculus acris	Meadow buttercup
Silene dioica	Red campion

Appendix 2.2: Width of floral units of *Rubus fruticosus* and *Centaurea nigra*

Rubus fruticosus data collection information

For *Rubus fruticosus*, 10 floral units were selected at chest height every 1m along the hedge section/

Width (cm) = The width of each floral unit taken from the top of the flower to the bottom when facing the hedge.

Date of data collection = 20/07/2020

Time of data collection = 11.52

Weather = 3.5 MPH wind, ~60% clear, 16.0 degrees C

Table A2.2_1 Width of *Rubus fruticosus* floral units (cm)

***Rubus fruticosus* floral unit**	**Width**
1	2.15
2	1.36
3	2.61
4	2.05
5	1.82
6	1.81
7	1.84
8	1.54
9	1.78
10	1.96
Mean	1.89
Variance	0.12

Centaurea nigra data collection information

For *Centaurea nigra*, 11 floral units were collected from two fields. A 1mx10m margin section had been marked out per field with each section divided into 10 $1m^2$ quadrats. The width of one *Centaurea nigra* floral unit per quadrat was measured unless there were no *C. nigra* units within a quadrat.

Width (cm) = The width of each floral unit taken from the top of the flower to the bottom when facing the direction of travel of the margin.

Information for Centaurea nigra units 1-5 (Field 2)

Date of data collection = 02/08/2020

Time of data collection = 09.12

Weather = 6.5 MPH wind, ~80% clear and sunny

Information for Centaurea nigra units 6-11 (Field 1)

Date of data collection = 02/08/2020

Time of data collection = 15.54

Weather = 3.8 MPH wind, ~60% clear and sunny, 22.0 degrees C

Table A2.2_2 Width of *Centaurea nigra* floral units (cm)

***Centaurea nigra* floral unit**	**Width**
1	2.38
2	1.35
3	1.02
4	1.3
5	1.86
6	2.55
7	2.8
8	3.79
9	2.67
10	3.28
11	3.47
Mean	2.41
Variance	0.86

Appendix 2.3: Selecting remote sensing units to map on the ground

Two margin sections were marked out within the study area, 6m wide from the crop/margin edge. *Silene dioica* had a spatially clustered pattern of flowering, i.e. it grew abundantly in a few clusters spaced far apart across the two margin sections. There were also a few individual remote sensing (RS) units (see Section 2.3 in main paper for definition) that were not part of any cluster. In order to relatively systematically select the *S. dioica* RS units to map on the ground, the length of each margin section was walked. If an individual RS unit was encountered it was mapped. Each time a cluster of *S. dioica* RS units was encountered, when standing in front of the cluster in the direction of travel along the margin, the furthermost RS units at the top, right, bottom and left of the cluster were mapped. The idea was that the approximate area of the whole cluster could later be located within the imagery if individual RS units were not visible.

For clusters where mapping only the top, left, bottom and right RS units would leave a big gap in the centre of the cluster, a few additional RS units were mapped around the edge (see Figure S3.1).

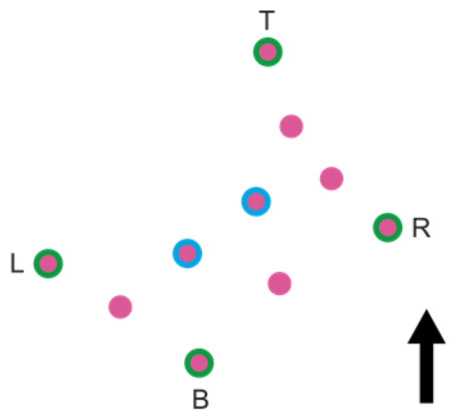


Figure S2.1 *Silene dioica* remote sensing (RS) units in an example cluster. Those labelled T, R, B and L and highlighted in green are the RS units that are the furthest to the top, right, bottom and left of the cluster respectively and the ones that would be mapped. So as to avoid a large gap in the cluster between the L and T floral units, additional RS units would also be mapped (those circled in blue). The fieldworker's direction of travel along the margin is shown by the black arrow.

In July, *Centaurea nigra* was growing abundantly and fairly evenly spread across the two margin sides. As such, clusters of *C. nigra* merged into one another and were not separable. To therefore make sure that *C. nigra* RS units in different parts of the margin were sampled, each margin section was divided into sub-sections 10m in length and 6m in width from the margin/crop edge. The locations of the first 12 RS units in each sub-section were mapped before moving on to the next sub-section. Due to the abundance with which *C. nigra* was growing across each margin, the 12 RS units marked out within each sub-section were clustered closely together, often within a much larger patch of *C. nigra*. They would therefore show us the starting location of that patch of *C. nigra* RS units, even if individual RS units could not specifically be identified within the imagery.

Appendix 2.4: Locating RS units within the remotely sensed imagery

Using GPS for collecting field data is a standard procedure within remote sensing research (e.g. see Fisher et al., 2018). A GPS receiver with an accuracy within several metres was not feasible for this study which was looking to capture ground data in some instances only several centimetres wide, for example individual *Centaurea nigra* remote sensing (RS) units.

Two alternative methods were employed. Firstly, ground-control points (GCPs) were established. Standard classroom whiteboards (~60cm length x 40cm width) were used as GCPs. These were placed every 20m along the margin and 3m in to the margin from the crop/margin edge. Markers were placed at three corners of the GCP boards and along the margin in between each GCP board. The distances of each marker from the GCP boards had been established.

A DeWALT laser beam measure (±1 digit accuracy) was used to determine the distance of floral units from a minimum of two markers. At a later stage this allowed the location of floral units within the imagery to be determined. In QGIS version 3.4.15 (QGIS, 2020), buffers with radii equal to the distances measured between floral units and markers were drawn around each marker respectively. Buffer intersections were used to calculate floral unit locations (See Figure S3.2).

Secondly, a Topcon Real-time Kinetic (RTK) HiPer V receiver was used for gathering waypoints. RTKLIB version 2.4.2 software (RTKLIB, 2013) was used to convert waypoint data into a KML vector file, a format that can be uploaded into QGIS.

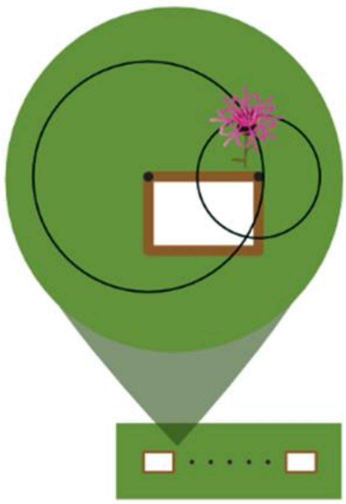


Figure S2.2. Locating a *Centurea nigra* remote sensing unit using buffers (not to scale) Lower: Black points demonstrate the position of markers between whiteboard ground-control points (GCPs). In the expanded section, markers can also be seen in the corners of GCPs. They also mark the centre of each buffer. The distance measured between a marker and the centre of the floral unit serves as the radius of each buffer. Buffer intersections show the location of remote sensing units.

Appendix 2.5: Creating the accuracy assessment layer

For each individual image, 64 pixels belonging to each of the focal flowering plant species were purposively selected where possible, as ground-truth data were limited. For May and July 7cm images, only 25 pixels of data were available for *Silene dioica* and *Centaurea nigra* respectively. Different flower patches to those used within the training dataset were used for creating the accuracy assessment layer. Pixels horizontally or vertically adjacent to each other were not selected for inclusion as verification pixels to avoid any radiance spill over effects. However, in order to have enough pixels for *S. dioica* and *C.*

nigra within the accuracy assessments, pixels adjacent to each other on the diagonal were often selected (see Figure S2.3).

When creating a set of verification pixels for each of the flowering plant species of interest for which enough ground-truth data were available (*Prunus spinosa*, *Crataegus monogyna* and *Rubus fruticosus*), 32 'edge' pixels and 32 'pure' pixels were purposively selected in order to cover a range of spectral variability within a particular flowering plant species category.

Figure S2.3 *Centaurea nigra* verification pixels selected for inclusion within the July accuracy assessment. These are highlighted in black. Verification pixels could only be adjacent to one another on the diagonal.

An 'other' category was then created for the accuracy assessment layer for each month respectively. This contained 640 randomly selected verification pixels covering a range of different features from within the imagery, such as branches, machinery, foliage or dry vegetation. However, random selections within certain areas of the imagery were sometimes controlled so that only features that I definitely knew weren't flowering plant species categories of interest were included. For July for example, when randomly selected points fell outside the blue areas shown in Figure S3.4, only points that fell on white flowers or patches of shadow were included within the accuracy assessment. This is because I knew that the white flowering species in those areas definitely weren't *Rubus fruticosus* and it was assumed that no shadow pixels would be recognised as a particular flowering plant species of interest.

If there was uncertainty as to whether a randomly selected pixel could indeed be included in the 'other' category or whether it was a pixel belonging to one of the flowering plant species of interest, it was not included in the accuracy assessment and another pixel was randomly selected instead.

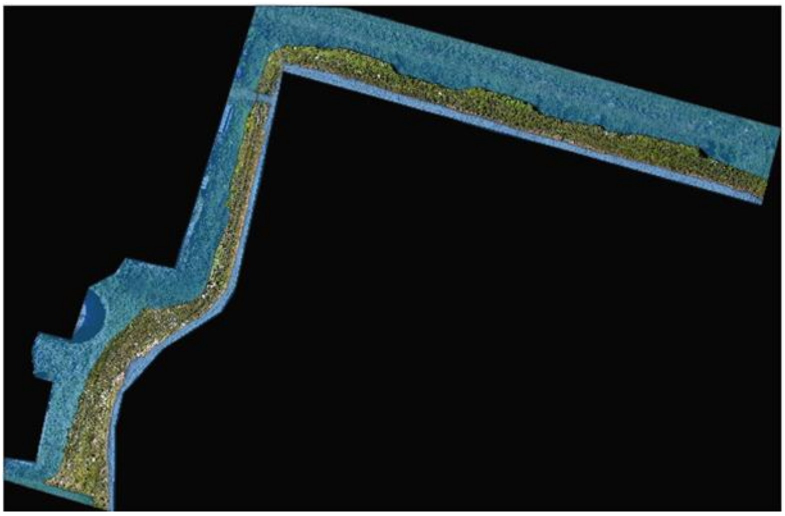


Figure S2.4 July 3cm resolution image showing the study site. Within areas highlighted in blue, verification pixels could be included across the whole area providing that they weren't *Rubus fruticosus* which was one of the flowering plant species of interest. Within areas not highlighted in blue, randomly selected verification pixels would only be included in the accuracy assessment layer if they clearly belonged to patches of white flowering species or shadow.

Appendix 3.1 List of species included in Kings Crops 'Basic Pollen and Nectar Mix KWM2bs'

Note: common name is in brackets.

- *Trifolium hybridum* (Alsike clover)
- *Centaurea nigra* (Common knapweed)
- *Lotus corniculatus* (Birdsfoot trefoil)
- *Malva moschata* (Musk mallow)

- *Vicia sativa* (Common vetch)
- *Silene dioica* (Red campion)
- *Leucanthemum vulgare* (Ox-eye daisy)
- *Trifolium pratense* (Red clover)
- *Onobrychis viciifolia* (Sainfoin)
- *Medicago lupulina* (Black medick)
- *Prunella vulgaris* (Selfheal)

Frontier Agriculture Ltd. (2021). ‘Basic Pollen and Nectar Mix KWM2bs’, URL: <https://www.kingscrops.co.uk/products/product/18-basic-pollen-and-nectar-mix> [Accessed: 27/09/2021].

Appendix 3.2: Sensitivity Analyses

I ran sensitivity analyses on the Bee$_{Hon}$ model to see whether variations in the nectar sugar values (mean mg/m^2/day) for some flowering plant species, for example if I had been uncertain as to a species identification, would lead to a different outcome. All of the sensitivity analyses led to the same overall outcome. I outline each of the sensitivity analyses carried out below.

Sensitivity analysis 1:

For species meeting the following criteria, I doubled the nectar sugar (mean mg/m^2/day) value included in the original Bee_{Hon} and Bee_{Wild} models:

- If I was not 100% sure which species a floral unit belonged to, but in the original model I had listed the species that it was most likely to belong to.
- If nectar values were only available for one genus member, and I had used that value for a member of a different genus.
- If I had identified a species and used the identification for other floral units that I thought were the same species in the field, but that may have potentially been another species of very similar appearance
- In one instance in Margin 3, I had not specified which *Cirsium* species a floral unit was in my notes, so I went with *Cirsium arvense*, but in sensitivity analysis I put *Cirsium vulgare* value which was the other potential option.
- *Lathyrus nissolia* was not present in either nectar database so I used the genus member with the most conservative nectar sugar value in the original model (*Lathyrus pratensis*). Then in Sensitivity analysis 1 I used the doubled nectar sugar value of the genus member with the least conservative nectar sugar value *Lathyrus latifolia*.

Table A3.2_1 Bee_{Hon} model run with nectar values adjusted according to Sensitivity Analysis 1

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.002**	**0.497**	**NA**	**Kept in final model**	**0.001***
Nectar sugar (mg/m²/day)[1]	**0.006**	**0.001**	**Continuous**	**Kept in final model**	**<0.001***
Margin type (NatReg/Kings)	NA	NA	Categorical	6	NA
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Table A3.2_2 Bee_{Hon} model run with nectar values adjusted according to Sensitivity Analysis 1 with influential points removed (margins 4 and 15).

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.970**	**0.308**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	6	NA
Margin type (NatReg/Kings)	**-1.872**	**0.746**	**Categorical**	**Kept in final model**	**0.028***
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	2	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	3	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Table A3.2_3 Bee$_{\text{Wild}}$ model run with nectar values adjusted according to Sensitivity Analysis 1

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**3.085**	**0.173**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)[1]	NA	NA	Continuous	5	NA
Margin type (NatReg/Kings)	**-1.668**	**0.433**	**Categorical**	**Kept in final model**	**0.002***
Mean temperature (°C)	NA	NA	Continuous	6	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Sensitivity analysis 2:

For species meeting the following criteria, I halved the nectar sugar value included in the original Bee_{Hon} and Bee_{Wild} models:

- If I was not 100% sure which species a floral unit belonged to, but in the original model I had listed the species that it was most likely to belong to.
- If nectar values were only available for one genus member, and I had used that value for a member of a different genus.
- In one instance in Margin 3, I had not specified which *Cirsium* species a floral unit was in my notes, so I went with *Cirsium arvense*, but in sensitivity analysis I put *Cirsium vulgare* value which was the other potential option.
- *Lathyrus nissolia* was not present in either nectar database so I used the genus member with the most conservative nectar sugar value in the original model (*Lathyrus pratensis*). Then in Sensitivity analysis 2, I halved the nectar sugar value.

Table A3.2_4 Bee_{Hon} model run with nectar values adjusted according to Sensitivity Analysis 2

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.016**	**0.485**	**NA**	**Kept in final model**	**0.001***
Nectar sugar (mg/m²/day)	**0.007**	**0.001**	**Continuous**	**Kept in final model**	**<0.001***
Margin type (NatReg/Kings)	NA	NA	Categorical	6	NA
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Table A3.2_5 Bee$_{Hon}$ model run with nectar values adjusted according to Sensitivity Analysis 2 with influential points removed (margins 4 and 15).

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.970**	**0.308**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	6	NA
Margin type (NatReg/Kings)	**-1.872**	**0.746**	**Categorical**	**Kept in final model**	**0.028***
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	2	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	3	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Table A3.2_6 Bee$_{Wild}$ model run with nectar values adjusted according to Sensitivity Analysis 2

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**3.085**	**0.173**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	5	NA
Margin type (NatReg/Kings)	**-1.668**	**0.433**	**Categorical**	**Kept in final model**	**0.002***
Mean temperature (°C)	NA	NA	Continuous	6	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Sensitivity analysis 3:

For species where my definition of a floral unit had been different to that of Baude et al. (2015), e.g. for *Prunella vulgaris* I had counted one stem as a floral unit whereas Baude et al. (2015b) had counted each individual *P. vulgaris* flower as a floral unit, I re-ran the model but multiplied the nectar value of each of those species by the maximum number of flowers potentially found in a floral unit at the study farm. This maximum number of flowers potentially found in a floral unit at the study farm had been identified through a separate survey carried out at the study farm, where I counted the number of flowers in my definition of a floral unit.

Table A3.2_7 Bee_{Hon} model run with nectar values adjusted according to Sensitivity Analysis 3

Variable / variable interactions	**Estimate**	**S.E.**	**Variable type/interaction type**	**Order of removal from model**	***p*-value**
Intercept	**2.000**	**0.486**	**NA**	**Kept in final model**	**0.001***
Nectar sugar (mg/m²/day)	**0.007**	**0.001**	**Continuous**	**Kept in final model**	**<0.001***
Margin type (NatReg/Kings)	NA	NA	Categorical	6	NA
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model.

S.E. stands for ‘standard error’

Significant *p*-values marked with a (*).

Table A3.2_8 Bee$_{Hon}$ model run with nectar values adjusted according to Sensitivity Analysis 3 with influential points removed (margins 4 and 15).

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**2.970**	**0.308**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	6	NA
Margin type (NatReg/Kings)	**-1.872**	**0.746**	**Categorical**	**Kept in final model**	**0.028***
Mean temperature (°C)	NA	NA	Continuous	5	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	2	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	3	NA
Margin type / Mean temperature	NA	NA	2-way interaction	4	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model

S.E. stands for 'standard error'

Significant *p*-values marked with a (*).

Table A3.2_9 Bee$_{Wild}$ model run with nectar values adjusted according to Sensitivity Analysis 3

Variable / variable interactions	Estimate	S.E.	Variable type/interaction type	Order of removal from model	*p*-value
Intercept	**3.085**	**0.173**	**NA**	**Kept in final model**	**<0.001***
Nectar sugar (mg/m^2/day)	NA	NA	Continuous	5	NA
Margin type (NatReg/Kings)	**-1.668**	**0.433**	**Categorical**	**Kept in final model**	**0.002***
Mean temperature (°C)	NA	NA	Continuous	6	NA
Nectar sugar / Margin type	NA	NA	2-way interaction	3	NA
Nectar sugar / Mean temperature	NA	NA	2-way interaction	4	NA
Margin type / Mean temperature	NA	NA	2-way interaction	2	NA
Nectar sugar / Margin type / Mean temperature	NA	NA	3-way interaction	1	NA

Note: Variables in bold are those that were kept in the final model.

S.E. stands for ‘standard error’

Significant *p*-values marked with a (*).

Appendix 3.3: Table of bee abundance in each margin at the study farm

Margin	Margin Type	Nectar sugar (mean $mg/m^2/day$)	Floral species richness	Total solitary bees	Total no. honeybees	Total no. bumblebees	Total wild bees	Total bees
1	NatReg	2.23	8	0	0	1	1	1
2	NatReg	1.07	4	0	0	0	0	0
3	NatReg	44.74	3	1	6	9	10	16
4	Kings	483.77	12	3	108	12	15	123
5	NatReg	38.61	3	1	1	0	1	2
6	Kings	263.98	12	3	45	9	12	57
7	NatReg	20.04	11	4	0	1	5	5
8	Kings	40.31	5	5	15	17	22	37
9	NatReg	39.97	6	1	6	0	1	7
10	NatReg	19.77	11	3	0	3	6	6
11	Kings	49.76	10	10	41	28	38	79
12	NatReg	15.36	10	5	11	4	9	20
13	Kings	130.07	10	4	1	9	13	14
14	Kings	136.73	10	15	3	4	19	22
15	Kings	318.56	11	19	166	24	43	209
16	Kings	133.81	8	9	12	4	13	25

Appendix 3.4: The proportion (%) of semi-natural habitat surrounding each margin at the study farm at a 250m radius

Margin	Proportion of semi-natural habitat (%)
1	1.62
2	3.19
3	12.59
4	1.12
5	1.28
6	3.05
7	29.35
8	1.15
9	8.29
10	13.51
11	3.79
12	28.94
13	30.88
14	0.00
15	3.86
16	1.72

Appendix 3.5: Analysing the proportion (%) of semi-natural habitat surrounding each margin at the study farm at a 500m radius

The percentage of semi-natural habitat in 500m radius buffers around each margin ranged between 0.7% and 27.3% (see Table A3.5_1 below). No difference ($W = 15$, $p = 0.083$, $n = 8$) was initially found between margin types (Kings and NatReg) when comparing the proportion of semi-natural habitat in 500m buffers (see Figure S3.1). When removing the outlier from the Kings mix however (Figure S3.1), semi-natural habitat proportion between the two margin types was significantly different ($W = 9$, $p = 0.029$). When the outlier was removed, mean proportions of 3.3% ± 1.5% (1 S.E., $n = 7$) and 12.1% ± 3.6% (1 S.E., $n = 8$) were found surrounding Kings and NatReg margins respectively. With the outlier removed, a median proportion of 8.3% semi-natural habitat was found in buffers surrounding NatReg margins and a median proportion of 1.3% was found in buffers surrounding Kings margins.

Table A3.5_1 The proportion (%) of semi-natural habitat surrounding each margin at the study farm at a 500m radius

Margin	Proportion of semi-natural habitat (%)
1	5.46
2	3.24
3	5.06
4	1.23
5	1.66
6	1.27
7	27.28
8	2.35
9	11.05
10	26.67
11	11.47
12	16.54
13	22.96
14	0.72
15	5.29
16	1.09

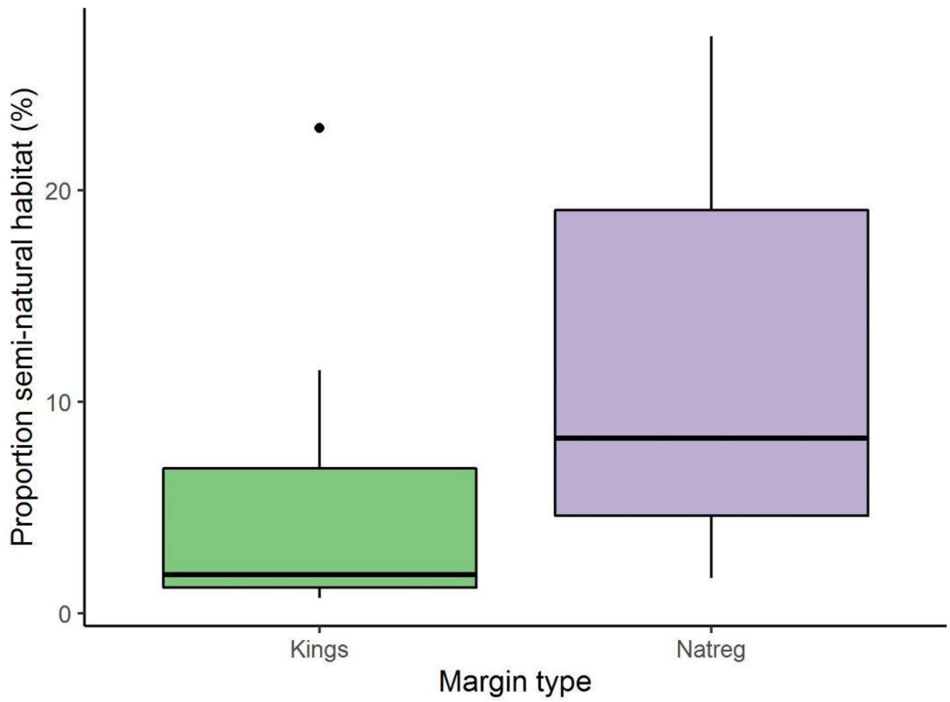


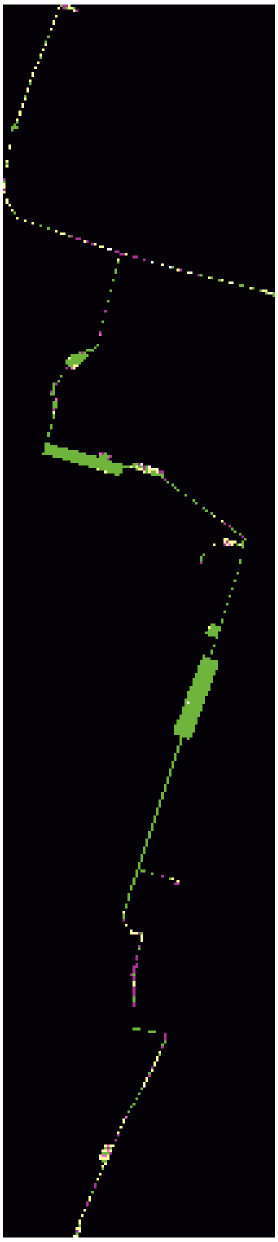
Figure S3.1 The proportion of semi-natural habitat in 500m buffers surrounding margin sections, according to each margin type (W = 15, p = 0.083, n = 8). Note that each box represents the interquartile range, the horizontal line in the centre of the box represents the median value and the whiskers represent the highest and lowest values respectively. The black point represents an outlier. If the outlier seen in the Kings mix is removed, the difference in the proportion of semi-natural habitat between the two margin types is significant (W = 9, p = 0.029).

Appendix 4.1 Composition of the Limagrain (AWF4) mix present in some of the study farm margins

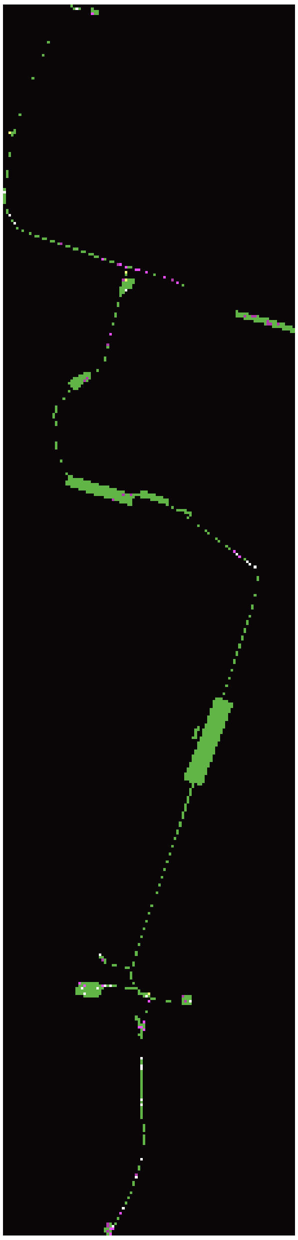
- **80% Grass Mixture**
  Browntop Bent - *Agrostis capillaris*
  Chewings Fescue *Festuca rubra commutata*
  Crested Dogstail *Cynosurus crista*tus
  Sheeps Fescue *Festuca ovina*
  Slender Creeping Red Fescue *Festuca rubra litoralis*
  Smooth Stalked Meadow Grass *Poa Pratensis*
  Strong Creeping Red Fescue *Festuca rubra rubra*
- **20% Floral Mixture**
  Birdsfoot Trefoil *Lotus corniculatus*
  Bulbous Buttercup *Ranunculus bulbosus*
  Common Vetch *Vicia sativa*
  Knapweed *Centaurea nigra*
  Lady's Bedstraw *Galium verum*
  Lesser Trefoil *Lotus corniculatus*
  Oxeye Daisy *Leucanthemum vulgare*
  Salad Burnet *Sanguisorba minor*
  Self-heal *Prunella vulgaris*
  Teasel *Dipsacus fullonum*
  Wild Carrot *Daucus carota*

Limagrain. (2021) 'Our Products' <URL: https://www.lgseeds.co.uk/crops/> [Accessed: 31/12/2021]

Appendix 4.2 Example classifications for UAV_{Set1} and UAV_{Set2}



(a)



(b)

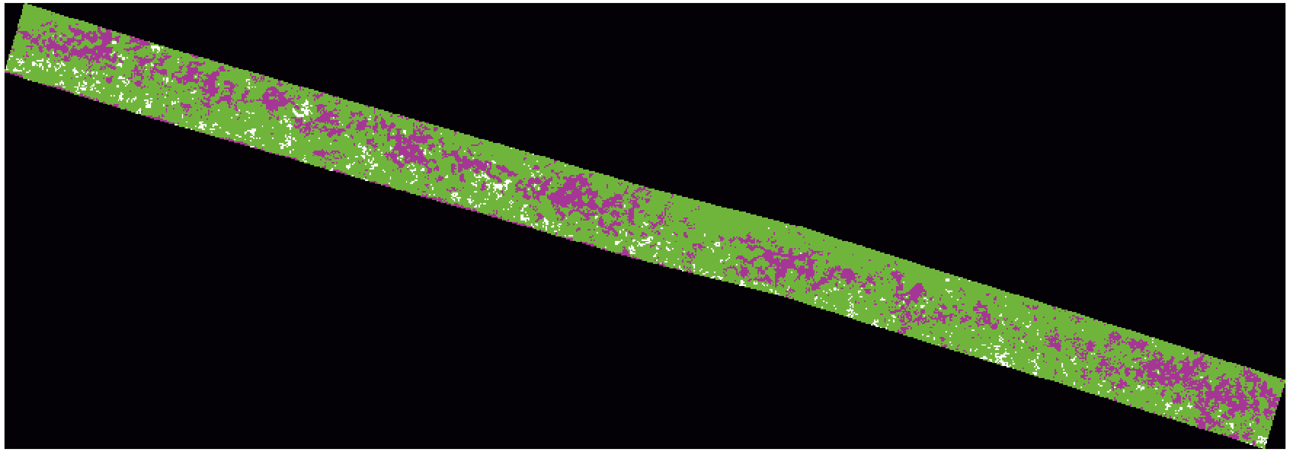
Figure A4.2_2 (a) Outline of the UAV_{Set1} classification iteration 4 and (b) UAV_{Set2} classification iteration 8

Appendix 4.3: Table showing adjustments made to each classification iteration for UAV_{Set1} and UAV_{Set2} respectively

Classification iteration	Training set alterations in classification iterations
UAV_{Set1}	
1	Extra values purposively added to the 'other' classification category to refine the classification algorithm where pixels were confused with flowering plant species. With *Chamerion angustifolium* and *Achillea*. *Centaurea nigra* pixels collated across two plots. *Leucanthemum vulgare* pixels collated across one plot.
2	Same as iteration 1 but without extra values added to the 'other' classification category.
3	Same as iteration 2 with 'edge' pixels added to *C. nigra* and *L. vulgare* (up to 50 edge pixels each),
4	Same as iteration 2 but with *L. vulgare* pixels collated across two margins rather than one. Note that doing this meant that we had to reduce the number of verification pixels included in the accuracy assessment from 64 to 53.
UAV_{Set2}	
1	Baseline classification iteration, including pixels originally selected for each classification category.
2	Same as iteration 1, with extra values purposively added to the 'other' classification category to refine the classification algorithm where pixels were confused with flowering plant species.
3	Same as iteration 2 but with training pixels selected across two plots each for *Centaurea nigra* and *Leucanthemum vulgare* rather than one plot. The second plot was the one established for UAV_{Set1} imagery originally and so only had very few *C. nigra* and *L. vulgare* floral units still flowering by the data of acquisition of UAV_{Set2} .
4	Same as iteration 2 but with even 'whiter' and 'pinker' training pixels selected for *Leucanthemum vulgare* and *Centaurea nigra* respectively. By whiter and pinker training pixels, we mean pixels that were even less likely to be mixed with other features in the centre of clusters of the relevant flowering plant species.
5	Same as iteration 1 but with even 'whiter' and 'pinker' training pixels selected for *Leucanthemum vulgare* and *Centaurea nigra*, as described under iteration 4.
6	Same as classification 5 but with additional values added in *Centaurea nigra* and *Leucanthemum vulgare* sections (extra 5 and extra 6 values).
7	Same as classification 4 but with additional values in *Centaurea nigra* and *Leucanthemum vulgare* sections (extra 5 and extra 6)

8	Same as classification 7 but with *Daucus carota* training and accuracy assessment pixels selected across two plots rather than one. To do this, we rearranged *D. carota* training and verification plots. We had originally established one training and one verification plot respectively. In order to select training pixels from both of these plots, we divided each plot into two sub-plots and used one sub-plot for selecting training pixels and one sub-plot for selecting verification pixels.
9	Same as classification 8 but with original *Centaurea nigra* pixels rather than 'pinkest' *C. nigra* pixels.
10	Same as classification 9 but with extra pixels added to the 'other' classification category.

Appendix 4.4 Example UAV$_{Set1}$ margin classification for Margin 4



Legend:

- Unclassified
- Other
- Achillea
- Willowherb
- Leucanthemum
- Centaurea

Appendix 4.5 Soil types in each of the 16 margins at the study farm

Margin	Topsoil texture
1	Heavy, silty clay loam
2	Medium clay loam
3	Medium clay loam / Sandy silt loam
4	Medium clay loam / Sandy silt loam / Medium silty clay loam
5	Medium clay loam / heavy, silty clay loam
6	Medium silty clay loam
7	Medium clay loam
8	Medium clay loam
9	Medium clay loam / Sandy, silt loam
10	Medium clay loam /sandy silt loam
11	Heavy, silty clay loam
12	Medium clay loam
13	Heavy, silty clay loam
14	Loamy sand
15	Medium silty clay loam / medium clay loam
16	Medium clay loam