Biodiversity and ecosystem services in fruit farms: the roles of management and semi-natural habitats.

© Natalia Zielonka: Blackbird *Turdus merula* sitting on vineyard trellis, in East Sussex, England.

Natalia Barbara Zielonka

Thesis submitted for the degree of Doctor of Philosophy

University of East Anglia

School of Biological Sciences

December 2023

I’d like to dedicate this thesis to my Grandparents –
Barbara and Eugeniusz Rogowscy.

It feels like you’ve been gone so long, yet your love still powers me through.
I know you would have loved to hear about my research.

Rest in Peace.

Abstract

Agriculture occupies 40% of the Earth's land, and habitat loss, landscape homogenisation and agrochemical use associated with agricultural expansion and intensification are leading biodiversity threats. Research is needed to inform a shift from agricultural land devoid of life, to biodiversity-rich landscapes that are managed in ways that maximise biodiversity's benefits to production and human wellbeing. In this thesis, we combine active bird and arthropod surveys and passive acoustic monitoring to study biodiversity responses to landscape and management variables across two relatively novel perennial agricultural systems: grape and mango farms in north-eastern Brazil, and vineyards in England. Firstly, we demonstrate that the expansion of fruticulture within the Caatinga biome has a detrimental effect on bird communities and may be fuelling the homogenisation of bird assemblages. Secondly, we show that organic management is not a sustainable approach to English viticulture, as we find organic vineyards to have significantly lower yields, but without consistent biodiversity benefits. Similarly, we show that accreditation through an industry sustainability scheme is not a reliable, nor an intuitive predictor of biodiversity benefits or of biodiversity-friendly management. Instead, we identify ecotoxicity derived from agrochemical use and ground vegetation cover to be the most important drivers of arthropod and bird biodiversity. Biodiversity can be associated with both benefits and costs to crop production, and through exclusion experiments, we show that under certain conditions, an influx of grape-eating bird species at harvest can significantly reduce yields, which optimised vineyard design and targeted management could address. Importantly, we demonstrate that visitors' experience of vineyard tours is enhanced by more complex soundscapes linked to higher bird species richness, and so bird conservation measures could help boost visitors' experience and contribute to business prosperity. Taken together, this thesis makes direct recommendations for incorporating biodiversity conservation into the management of perennial fruit farms and suggests how payment-driven schemes could support the delivery of these recommendations.

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Author contributions and publication summary

At the time of thesis submission, two of the four data chapters presented in this thesis have been submitted for publication and are under review, a third is near-submission and the fourth is being prepared for submission. Although I am the lead author of all chapters and made the largest contribution to each piece of work, I have received data, support and advice from various co-authors. Co-authorship and author contributions for each chapter are outlined below:

Chapter 2

Natalia B. Zielonka, Eduardo Arellano, Liam P. Crowther, Vinina Ferreira, Andrés Muñoz-Sáez, Patricia Oliveira-Rebouças, Fabiana Oliveira da Silva, Simon J. Butler & Lynn V. Dicks. **Distinct bird communities in fruit farm and forest patches across intensively managed fruit farm landscapes in the semi-arid Caatinga biome in north-eastern Brazil.** [*re-submitted to Ibis following minor revisions]*

> NBZ conceived the study and designed the methodology with support from SJB and LVD. NBZ collected the data, with support from LPC, VF, AMS, POR and FOS. Fieldwork was conducted across the SUFICA project sites in north-eastern Brazil and EA, VF, POR, FOS and LVD all made significant contributions to leading of the project, setting up collaborations with farmers and making data collection possible. NBZ led the data analysis and writing, with support from SJB and LVD. All co-authors gave final approval for submission.

Chapter 4

Natalia B. Zielonka, Jack D. Shutt, Simon J. Butler & Lynn V. Dicks. **Management practices, and not surrounding habitats, drive bird and arthropod biodiversity within vineyards.** *[received reviewer comments from by Agriculture, Ecosystems & Environment]*

> NBZ conceived the study and designed the methodology with support from SJB and LVD. NBZ collected and curated the data. NBZ led the data analysis with support from JDS and SJB. NBZ led on the writing with support from JDS, SJB and LVD, and all co-authors gave final approval for submission.

Chapter 5

Natalia B. Zielonka, Jack D. Shutt, Simon J. Butler & Lynn V. Dicks. **Bird communities and their contributions to ecosystem disservices interact with vineyard configuration and management to affect yield across English vineyards.** *[in preparation for submission to Ecological Applications]*

> NBZ conceived the study and designed the methodology with support from SJB and LVD. NBZ collected and curated the data. NBZ led the data analysis with support from JDS and LVD. NBZ led on the writing with support from JDS and LVD, and SJB provided comments.

Chapter 6

Natalia B. Zielonka, Victoria Tubman, Lynn V. Dicks & Simon J. Butler. **Louder and more diverse vineyard soundscapes, associated with higher bird species richness, increase visitors' tour experience.** *[ready for submission to People and Nature]*

> NBZ conceived and designed the methodology for the soundscape monitoring part of the chapter with SJB, and VT conceived and designed the methodology of the soundscape vineyard tour study with support from NBZ and SJB. NBZ collected and processed all acoustic data, and VT constructed the birdsong choruses and collected the soundscape vineyard tour study data with support from NBZ. NBZ led on data analysis and writing with support from SJB, and LVD provided comments on the chapter. All co-authors have given approval for submission.

Chapters 1 and 7 (general introduction and discussion, respectively) were written by Natalia B. Zielonka with comments from Prof Lynn Dicks and Dr Simon Butler. **Chapter 3** (vineyard study site selection) was led by Natalia B. Zielonka with support and input from Prof Lynn Dicks and Dr Simon Butler.

Acknowledgements

The last 4 years and 3 months have been a rollercoaster of life events and changes, not to mention the global pandemic, and completing this PhD thesis (or surviving) would not have been possible without the assistance, support, enthusiasm, friendship and love of so many people.

Firstly, I am incredibly grateful to my supervisors Lynn Dicks and Simon Butler for their ongoing support, guidance, patience and enthusiasm over the past 4 (and a bit) years, and without whom, this work would not have been possible, nor would I have become the scientist (*I think I'm officially one now, right?!)* I am today. You have both pushed me, challenged me, and most importantly, believed in me and my skills. Lynn – you have taken my interest in birds in your stride and have supported my research wherever I wanted to take it. Your interdisciplinary outlook on agroecology has been inspiring and has shaped the way I view my research. Simon – you have boosted my confidence, provided clarity and just made sense of things on so many occasions, preventing a fair few breakdowns! Working with you has been fun and your critical way of thinking and challenging the meaning of things will stay with me. I am also indebted to Jack Schutt, who has (unofficially but prominently) provided supervision, and friendship, over the past year. I am hugely grateful for your eagerness to wrap your head around my project and for taking the time to share your wisdom. I could always count on you to both, hack my statistical analyses apart (teaching me a lot on the way), and be a source of reassurance and laughter.

None of the work presented in this thesis would have been possible without the trust that farm managers over in Brazil and England have put into me and research. Sadly, my work in Brazil did not last long, but I feel very lucky to have had the opportunity to visit the amazing Caatinga and undertake work there. Thank you for entrusting a complete stranger from abroad to explore your farms, talk to you about birds and build tall wooden structures on your farms (perches)! The project across English vineyards came about unexpectedly, yet ended up shaping most of my PhD research, and has only been possible thanks to the excitement from vineyard managers that just wanted to know more about birds. I am hugely thankful to Chris Foss for helping get the UK vineyards project off the ground, and for our conversations that have shaped much of my work. I am also very grateful to all project vineyard managers who have made me feel incredibly welcome to wander around English vineyards and take note of anything that's flying or crawling, whilst allowing me to dig holes in your ground, put bags on your grapes and ask lots of questions!

Fieldwork has been eventful to say the least and I wouldn't have done it alone! I am grateful to Andrés for introducing me to the birds of Caatinga and for showing me the ropes across the

SUFICA farms, as well as to Gilson and Danilo for their help with fieldwork in Brazil. It is easy to feel lonely and lost in a foreign country, but you looked after me, pointed out venomous snakes and shared my joy of seeing many new and pretty species! Working over in Brazil would not have been possible without the SUFICA team, who worked hard to set up the project farms, and I am particularly grateful to Fabiana, Vinina and Patricia who have been on hand to help me communicate with farmers, translate protocols, guidance booklets and show me some of Petrolina. I may still be experiencing the side effects of swimming in the São Francisco River but going to Brazil was still one of the best things I've done so thank you to everyone who made it possible.

You'd think fieldwork in your home country would be easier, but life had different plans. In the earlier stages of this work, I had a plan to deploy armies of plasticine caterpillars (to measure biological pest control rates, not just for fun), which were the source of immeasurable stress. I am very appreciative to: Amy – for spending hours helping me create those armies, working out the best method of transporting said armies in a car for two weeks, and dealing with the despair that this has caused; Liam S. – for offering solutions to how it would be best to stick plasticine caterpillars to vine plants and giving me an icing syringe set to optimise caterpillar making, which wasn't strong enough for the plasticine but it provided inspiration to Dad, who I am grateful to for finding a suitable caulking gun that was robust enough to be loaded with green home-made plasticine and make thousands of caterpillars. Unfortunately, the plasticine caterpillars did not survive nature's elements, as rain turned them into sludge, whilst sun baked them. Anyway, we moved on and your efforts will not be forgotten. Everything for the UK vineyards project needed to happen *en masse* and Mum was always on hand to step in, painstakingly making hundreds of exclusion bags (huge thanks to Liam C. for the help with design!) with me and then joining me in the field in both years and so willingly helping me put them up and take them down! This list of fieldwork-related anecdotes could go on, but in the interest of time, I will move on acknowledge the following: Parents – thank you for lending me your car when mine was too small to fit hundreds of bags and then could take no more fieldwork (RIP Fabia, you were a trooper!); Liam S. and Amy – apart from general friendship, thank you for driving me around and helping me dig pitfall traps when I had long covid; Maddie – for your help in fieldwork.

Some of the best aspects of doing the PhD have been the community of wonderful people that I've become part of, namely UEA's Caterpillar Office, the Strangles gang, BIO 01 Floor, Cambridge's Agroecology group, and the BOU. In particular, I would like to mention a few people: Emily (tea making trips, always caring and being there to chat to), Mike (for complimenting my tea making skills and my snack choices… in seriousness, it's been fab sharing the office from day one, always great to chat and solve R issues together), Ginny (runs!), Ram (being one of the friendliest people I've ever met), Alex S. (we've done it together from day one to today's submission, survived all cohort meetings, and we both made it through the life and work-related ups and downs), Nathan (great to whinge and inspire kids with), Harry (curlew content, driving me to Liverpool and to Edinburgh, and back, in record times, and reliably someone to vent to), Elie and Midge (conference adventures, Cambridge trips, a group of mutual support – I'm finally joining you on the other side!), Jenn (always willing to listen and provide support), Claire (appreciating my photos of C&D and sharing photos of your pooch, for everything R-related, surviving Latitude together, grounding chats and a fun person to be around), Jenny G. (being one of the most inspiring, coolest and kindest scientists I've met), Johnny (always being friendly), Cat (cake, chocolate, coffee, R and cute photos), Rob (inspiring me to embark on this PhD journey and thorough chats about my work over pints), and Steve (welcoming me into the global ornithological family).

I'd also like to thank Duncan Westbury and Richard Davies for an enjoyable viva, full of in-depth discussions about my work. I am grateful for the time you took to read this thesis in detail and for spotting all the little typos and missing commas!

To successfully complete a PhD means I've had to survive life over the past few years, and in this respect, a few people deserve a mention.

Amy and Liam S. – our friendship, wildlife, coffee and pub trips have helped me get through the years, even the misery of covid. Thanks for always being on hand to teach me English too.

Rose – you looked after me in my lowest moments, provided love and care and even travelled to Kent with me on fieldwork to make sure of this! You've been reliably there to deal with existential crises caused by everything from PhD-related disasters to leaves falling off a tree.

John – you've brought love and happiness to my life over the past 18 months. I'm not sure you knew what you were getting yourself into, but you've been a rock to me whilst I cried a significant number of tears, and yet you always somehow managed to get a smile out of me. You've told me I'd smash it, and I guess I just did, so you're right once again…

Parents – mamo & tato – you have been a source of unconditional love and support not only over this PhD, but also over my entire life. I am eternally grateful for you both - I would not have achieved this without you.

Chapter 1: General Introduction

© Natalia Zielonka: fruit farms in the Caatinga forest, Brazil (top); English vineyard, West Sussex

Natalia B. Zielonka

1.1. Biodiversity loss in the Anthropocene

The Anthropocene is characterised by profound detrimental impacts of human activity on nature (Lewis & Maslin 2015), and continual and pervasive biodiversity declines are associated with it (Díaz *et al.* 2019, IPBES 2019). Just between 1970 and 2018, global animal populations monitored as part of the Living Planet Index have declined by an average of 68%, with declines being highest across Latin America at 92%, and much lower across Europe and North America, where they averaged 19% (WWF 2022). The declines are strong across taxa (WWF 2022), with increasing awareness that they may be as severe for invertebrates as for vertebrates (Dirzo *et al.* 2014, Hallmann *et al.* 2017), and even for 'common' species (Inger *et al.* 2015, Ceballos *et al.* 2017). These declines are mirrored in high extinction rates (Pimm *et al.* 2014), and as the list of known and assessed species is just a fraction of the species living on the planet (Turvey & Crees 2019), it is estimated that about one million animal and plant species are threatened with extinction (Díaz *et al.* 2019, IPBES 2019). The key drivers of biodiversity loss are land-use change, mostly associated with agricultural expansion and urbanisation, climate change and overexploitation by humans (Jaureguiberry *et al.* 2022). These patterns in biodiversity loss and extinction rates will continue to increase for as long as the human demand for food and space grows (Monroe *et al.* 2019, Andermann *et al.* 2020).

1.2. Agriculture in the centre of biodiversity loss – key patterns

Almost 40% of world's ice-free land is dedicated to agriculture, making it the single largest form of land-use (Ellis & Ramankutty, 2008). As the human population is still increasing, and with it, the demand for goods, it is predicted that 70-100% more food will need to be produced by 2050 compared to the 2010 levels (Godfray *et al.* 2010). Humanity's growing demand for agricultural produce is putting continual pressure on ecosystems around the world and despite decades of awareness of the detrimental impacts of agriculture on biodiversity (Millennium Ecosystem Assessment, 2005), the threats of agricultural expansion and intensification for global biodiversity are not showing signs of decline (Tilman *et al.* 2011). For example, from 2003 to 2019, global cropland area increased by 9%, with rates as high as 39% in South America, whilst the net-primary productivity, which is a measure of energy production per unit area of cropland, has increased by 25% in the same time period (Potapov *et al.* 2022).

1.2.1. Driver 1: Habitat loss

Agriculture is the single biggest driver of land-use change and destruction worldwide (Newbold *et al.* 2015), and it accounted for around 80% of global deforestation between 2000 and 2010 (Campbell *et al.* 2017). Agricultural expansion leads to habitat loss and landscape fragmentation, both of which are leading causes of biodiversity loss (Foley *et al.* 2005, Beyer & Manica 2019, Andermann *et al.* 2020). The importance of semi-natural habitat patches and isolation differ across taxa, for example, fragmentation and the loss of connectivity usually has a stronger negative effect on larger-bodied, more mobile taxa, such as birds, compared to invertebrates which rely on smaller patches of habitats (Bailey *et al.* 2010, Hall *et al.* 2022). Maintaining heterogeneity is key to supporting biodiversity across agricultural land (Benton *et al.* 2003, Bailey *et al.* 2010), both at landscape scales where semi-natural habitats mostly benefit larger-bodied taxa (Dicks, *et al.* 2013, Kormann *et al.* 2015, Ramos *et al.* 2018, Redlich *et al.* 2018, Adorno *et al.* 2021), and at local scales where small habitat patches are important for invertebrate biodiversity (Riva & Fahrig 2022). Beyond the area of semi-natural habitats, loss of landscape connectivity is a further threat to biodiversity (Fahrig 2017, Grande *et al.* 2020), and retaining landscape heterogeneity and connectivity under agricultural expansion can limit the resulting biodiversity declines (Chaplin-Kramer *et al.* 2015, Ramos *et al.* 2018).

1.2.2. Driver 2: Intensification

Agricultural intensification, which is characterised by homogenisation of agricultural landscapes and increased reliance on agrochemicals, has successfully increased yields, but at severe costs to biodiversity (Burns *et al.* 2021). Synthetic agrochemicals are a driver of biodiversity declines across taxa (Stehle & Schulz 2015, Beaumelle *et al.* 2023, Nicholson *et al.* 2023, Rigal *et al.* 2023), with evidence of their negative effect for human health (Nicolopoulou-Stamati *et al.* 2016). Agrochemicals are toxic to biodiversity and can result in direct killing of non-target invertebrates (Hallmann *et al.* 2017, Nicholson *et al.* 2023), or indirectly, by reducing the food availability for insectivorous species (Hallmann *et al.* 2014, Bowler *et al.* 2019). The effects of agrochemicals are higher in simple landscapes likely due to increased exposure to the agrochemicals, caused by a lower availability of alternative resources, or refuge areas, which forces populations to depend more strongly on the farmed habitats (Nicholson *et al.* 2023). Moreover, intensification is also associated with modernisation, such as building renovation that removes nesting opportunities for species, whilst more secure grain storage and moving animal farming indoors, has reduced 'spill-over' of food sources that farmland-associated bird species benefited from (Cabodevilla *et al.* 2021, Rosin *et al.* 2021).

1.2.3. Beyond biodiversity loss: altered communities

Agriculture leads to landscape homogenisation, which translates to the homogenisation of assemblages (Jongman 2002, Karp *et al.* 2012), as species that can adapt to modern intensive agriculture become more abundant. For example, farmland-associated bird species have undergone greater widespread declines relative to bird species associated with other habitats (Robinson & Sutherland 2002, Heldbjerg *et al.* 2018, Lees *et al.* 2022), whilst red-listed invertebrate taxa were more strongly affected by farm management than 'unthreatened' species (Kormann *et al.* 2015). This is partially explained by species' traits, as habitat or food-specialist species are more likely to decline, in favour of a less-diverse set of species that are generalist and occupy wider niches (Blackburn *et al.* 2009, Newbold *et al.* 2013, Val *et al.* 2018, Tucker *et al.* 2021). The latter group of species are better able to adapt to the changing conditions and invade novel or altered habitats (e.g. Doherty *et al.*, 2016; Hradsky *et al.*, 2017; Sofaer *et al.*, 2020). The outcome of these shifts is homogenisation of wild communities and natural ecosystems (Tabarelli *et al.* 2012).

1.3. Impacts on ecosystem functioning

1.3.1. Ecosystem services

The profound loss of biodiversity alters the functioning of ecosystems and the provision of goods and services on which human livelihoods and wellbeing rely (e.g. Díaz *et al.*, 2006; IPBES, 2019; Keping, 2023; WWF, 2022). Ecosystem services are natural resources and processes that benefit humans. There are four types of services: (i) direct goods from nature, or *'provisioning services'*, such as food; (ii) delivery of '*regulating services'* that occur in ecosystems, such as biological pest control, (iii) direct benefits of nature to human culture and wellbeing through '*cultural services',* and (iv) delivery of '*supporting services'*, such as habitat for wildlife, without which other ecosystem functions would not be possible.

There is a strong understanding of how biodiversity loss affects ecosystem functioning and human livelihoods (Díaz *et al.* 2006, Cardinale *et al.* 2012). The Millennium Ecosystem Assessment (2005) provided the first formal appraisal of the relationship between ecosystem functioning and human wellbeing, stating that optimising ecosystems to intensify the delivery of provisioning services (e.g. food) has simplified the structure of ecosystems, reducing their ability to deliver the other types of services. Ecosystem services are crucial for agriculture, for example, over 75% of global food crop types rely on animal pollination to some extent (IPBES 2019), whilst biological pest control was estimated to reduce crop damage by insect pests by up to 65% (Losey & Vaughan 2006). An unambiguous positive relationship between biodiversity, ecosystem functioning and its stability has been well-documented, however, the relationship is not linear and the loss of functioning accelerates with the progressive loss of diversity (Cardinale *et al.* 2012, Senapathi *et al.* 2021). Ecosystem functioning is underpinned by ecosystem services, and the direct relationship between biodiversity and ecosystem services has also been demonstrated. For example, it has been shown that provisioning services (including crop yields) and the stability of regulating services (including ecosystem resilience to change) are enhanced by greater biodiversity (Cardinale *et al.* 2012, Meyer *et al.* 2016).

The delivery of ecosystems services is dependent on semi-natural habitats and affected by farm management practices, so service delivery also varies spatially and temporally (e.g. Ryan *et al.* 2023). Practices associated with agricultural intensification, such as landscape homogenisation and agrochemical use, have a persistent detrimental effect on biological pest control (Geiger *et al.* 2010, Chaplin-Kramer *et al.* 2015, Rusch *et al.* 2016, Boesing *et al.* 2017, Dainese *et al.* 2019) and have been linked to increased pest outbreaks and insecticide use in vineyards (Paredes *et al.* 2021). However, whilst landscape complexity does explain a significant proportion of the variation in crop damage, the rates of biological pest control and their impact on yield are not consistent globally (Karp *et al.* 2018). The inconsistent patterns may arise for a few reasons: (i) pest and natural enemy abundances and activity are temporally variable so annual patterns may be masked by seasonal or interannual variation (e.g. Chaplin-Kramer *et al.*, 2013); (ii) pests and natural enemies may respond more strongly to landscape configuration than composition (e.g. Martin *et al.,* 2016); (iii) the effects of landscape composition could be masked by the variation in on-farm management that also affects service provision and can interact with landscape (Power 2010, Olimpi *et al.* 2020); and (iv) responses to landscape composition and configuration vary between different species of pests and natural enemies (Tscharntke *et al.* 2016). Together, these complex patterns limit the generalisation of findings across scales.

1.3.2. Ecosystem disservices

There are instances where increased biodiversity has detrimental effects on functioning and service provision. For example, increased biodiversity has been linked to reduced yields (e.g. Letourneau *et al.*, 2011), whilst diverse animal assemblages can reduce natural pest control through intra-guild predation (Vance-Chalcraft *et al.* 2007), and inflict direct crop damage (Zhang *et al.* 2007). Such interactions with biodiversity that negatively affect ecosystem functioning or human wellbeing are termed '*ecosystem disservices'*. Just like ecosystem services, disservices vary spatially and temporally, and can be higher in simple landscapes (Gonthier *et al.* 2019, Gagic *et al.* 2021, Smith *et al.* 2022). This means that the net effect of biodiversity on production is complex and context-dependent, resulting from trade-offs between multiple services and disservices, each of which can be affected by landscape and management factors (Bennett *et al.* 2009, Cardinale *et al.* 2012, Gonthier *et al.* 2019, Olimpi *et al.* 2020). In line with expectations, recent research that considered the net effects of biodiversity for production has found more positive outcomes in complex compared to simple landscapes, with positive effects on yield (Olimpi *et al.* 2020, Gagic *et al.* 2021). Nonetheless, comprehensive studies that consider the net outcome of biodiversity, and the simultaneous and relative effects on landscape complexity and on-farm management practices on their provision remain rare (Power 2010, Peisley *et al.* 2015, Pejchar *et al.* 2018).

1.4. Reconciling agriculture with biodiversity

1.4.1. Land-sharing vs. land-sparing paradigm

For much of this century, balancing biodiversity conservation and agricultural production has been viewed as a trade-off between the 'conflicting' scenarios of land-sharing *versus* land-sparing (Balmford *et al.*, 2005; Green *et al.,* 2005; Kremen, 2015). The debate concerns how land should be best allocated between agriculture and conservation to achieve the necessary productivity, whilst maintaining highest biodiversity. On one hand, the land-sharing strategy proposes to manage landscapes for both agriculture and biodiversity conservation, which would promote 'nature-friendly' approaches such as organic management and incorporating small patches of semi-natural habitats into agricultural landscapes (Kremen 2015). On the other hand, the land-sparing strategy advocates complete separation of land for farming and nature conservation. It proposes that food should be produced as intensively as possible and on the smallest possible land area to 'spare' the rest for nature and so, reducing the need for expansion (Phalan *et al.* 2016).

The debate has had a prominent place within conservation literature (e.g. Fischer *et al.,* 2008; Phalan *et al.,* 2014, 2016; Tscharntke *et al.,* 2012), though the number of empirical studies that explicitly compare biodiversity responses under sparing and sharing scenarios remains low (e.g. Edwards *et al.*, 2021; Grau *et al.*, 2013). Syntheses of literature and meta-analyses have failed to find unambiguous results supporting one strategy across spatial scales and taxa (e.g. Barral *et al.*, 2015). In a literature review, Grau *et al.* (2013) noted that evidence favouring each strategy comes from different types of systems. Sharing is supported within luxury goods production (e.g. livestock systems and cocoa and coffee plantations) where moderately high yields can be produced by systems high in biodiversity (e.g. Wurz *et al.*, 2022), whilst the production of essential goods that account for most global calories (oils and cereals) favours sparing which achieves highest yields through monocultures with high levels of artificial inputs (e.g. Phalan *et al.*, 2011). The outcome of each strategy is variable across systems, depending on the species present and their contributions through ecosystem services (and disservices), meaning that a single strategy is unlikely to work across all crop types.

Despite the loss of biodiversity on intensively managed agricultural land, there is extensive support for agricultural intensification as a means to reduce the environmental impacts of agriculture (Balmford *et al.*, 2019; Zabel *et al.*, 2019), and as the 'win-win' solution for meeting global food demands and conserving biodiversity (Tilman *et al.* 2011, Tscharntke *et al.* 2012). More recently, it has also been shown that increased biodiversity resulting from ecosystem recovery on spared land was mirrored in the recovery of ecosystem services, which agricultural landscapes could benefit from (Barral *et al.* 2015). Nonetheless, a lot of the evidence supporting land-sparing comes from taxa and species that require large fragments of continuous habitats to survive, such as birds and large mammals (e.g. Gilroy *et al.*, 2014; Kamp *et al.*, 2015; Phalan *et al.*, 2011, 2016), and a lot of the support comes from extreme examples of land sparing and sharing (Balmford *et al.*, 2019), where sparing achieves high yield on the farmed land and spared land is effectively managed for biodiversity.

Payment-driven incentive schemes for biodiversity-friendly farming practices, which align with the land-sharing strategy, have underpinned most conservation efforts within agricultural landscapes. For example, agri-environmental schemes (AES), which offer farmers compensation for adopting sustainable management, have been the main source of nature conservation funding across the European Union; in 2012 alone, the European Commission spent €3.2 billion in AES payments (Batáry *et al.* 2015). Some recent studies have demonstrated AES to benefit multi-taxa biodiversity (Boetzl *et al.* 2021, Redhead *et al.* 2022), but there are also many examples where they have not been effective, or had mixed effects (Kleijn *et al.* 2006, Fuentes-Montemayor *et al.* 2011, MacDonald *et al.* 2019, Sharps *et al.* 2023). This may be because AES promote generalisation of management approaches, and their effectiveness is dependent on the structure and management of surrounding landscapes, being generally more effective in simple rather than complex landscapes (Batáry *et al.* 2010). Evidence informing conservation actions needs to be specific and gathered across meaningful scales (Dolman *et al.* 2012, Smart *et al.* 2012), and this can then lead to effective recommendations that target specific species or functional groups, which leads to increased conservation success (e.g. Perkins *et al.* 2011, Bright *et al.* 2015, Boetzl *et al.* 2021). Another reason for the inconsistent and limited effectiveness of AES is that they form a small part of European Union’s Common Agricultural Policy (CAP), which allocates proportionally more funding to farmers for intensifying production, whilst the uptake of AES is voluntary and the design and implementation of the biodiversity supporting measures is left to the responsibility of individual countries (Reif & Vermouzek 2019). This means that the detrimental effects of intensification may outweigh any benefits of biodiversity measures, as observed in the steep bird population declines in Czechia after it entered EU’s CAP, which led to rapid agricultural intensification (Reif & Vermouzek 2019). Moreover, AES-funded flower fields surrounding agricultural land hosted different assemblages of invertebrates to those in semi-natural grasslands (Boetzl *et al.* 2021), suggesting that the benefits of AES-supported measures may be limited to farmland species. Taken together, this shows that AES prescriptions alone will not address the biodiversity losses associated with agriculture and stresses the need for maintenance of land that is solely dedicated to nature.

Organic agriculture sits on the land-sharing side of the paradigm because it tends to enhance the biodiversity within agricultural areas, with a yield penalty on a per hectare basis. Its uptake has been rising globally; in 2022, 1.6% of global agricultural land was organically managed (Willer & Lernoud 2017), whilst European Union's 'EU Green Plan' has set a target for at least 25% of EU's agricultural land to be organically managed by 2030 (European Commission 2023). Organic management eliminates the use of synthetic inputs, and its goal is to promote and enhance ecosystem functioning, including biodiversity. Overall, organic management increases multi-taxa richness and abundance across farmland (Tuck *et al.* 2014, Smith *et al.* 2020), whilst also having a positive effect on soil organic matter and microbial activity (Tuomisto *et al.* 2012, Lori *et al.* 2017). However, the results are mixed across taxa and studies, being generally more positive for plants and arthropods than for birds (Tuck *et al.*, 2014), being stronger in more homogenous and intensively-managed agricultural landscapes (Smith *et al.* 2020), and stronger when viewed at the field than farm scale (Schneider *et al.* 2014). This highlights the importance of studies considering the impacts of farming on biodiversity at multiple scales.

A concern for organic agriculture, and for wildlife-friendly farming practices more generally, is that they are associated with lower overall agricultural yields due to land being taken out of production or farmed less intensively. A recent meta-analysis that compared yields of conventional and organic farms across multiple crop systems found 18.4% lower yields in organic farming (de la Cruz *et al.* 2023), which agreed with earlier findings (de Ponti *et al.* 2012, Seufert *et al.* 2012). In fact, the relative size of biodiversity gain through organic agriculture is similar to yield loss (Gong *et al.* 2022). This is highly contextual however, as yield gaps between organic and conventional farming were significantly higher in warm temperate climates, and for oil, cereal and vegetable crops, whilst there was no significant yield gap for fruit, nut and sugar crops (Gong *et al.* 2022, de la Cruz *et al.* 2023). Moreover, yield from organic farming has significantly lower temporal stability compared to conventional agriculture (Knapp & van der Heijden 2018), which reduces its viability as a sustainable option for agriculture, especially under climate change scenarios that already threaten yield stability (Rezaei *et al.* 2023).

1.4.2. Reconciling sparing and sharing – multifunctional landscapes and ecological intensification

Land-sparing and land-sharing strategies have been mostly discussed as mutually exclusive and conflicting, whilst a mix of approaches is most likely to benefit a wider diversity of species. For example, a comparison of land management scenarios along a continuum between extreme land-sparing to extreme sharing found differences in which approach worked for different breeding birds, as some farmland species did best under low-yielding farmland (Finch *et al.* 2019). Rather, mixed approaches to landscape management have been proposed, such as three-compartment sparing (Finch *et al.* 2019), and management for 'multifunctional' landscapes (Grass *et al.* 2019). Such landscapes would cater for the conflicting needs of production and different species' habitat requirements: high-yielding farmland that meets the bulk of production demands, spared land that is managed as semi-natural habitat, and spared land that is managed as low-yielding farmland.

In recent years, the thinking has moved away from sparing *versus* sharing and instead focused more on enhancing the sustainability and resilience of agricultural systems through the maintenance of ecosystem services and ensuring stability of production (Kremen & Merenlender, 2018). Kremen & Merenlender (2018) have suggested to refocus the debate away from food production alone, and towards the concept of '*working landscapes',* also referred to as *multifunctional landscapes*, that deliver benefits for nature and people. Similarly, the concept of *'ecological intensification'* has become quite prominent, which proposes a focus on enhancing yields by harnessing nature's contributions to agriculture and by minimising the need for artificial inputs (Bommarco *et al.*, 2013). This approach would see a shift from agricultural land devoid of life, to biodiversity-rich land that is managed in ways that maximise biodiversity's benefits to production, and results in higher, or maintained yields but with reduced environmental impacts.

Diversification of farming to enhance ecosystem service provision is key to ecological intensification. Many diversification practices have been demonstrated to successfully enhance biodiversity and ecosystem service provision (Kremen & Miles 2012, Garbach *et al.* 2017, Rosa-Schleich *et al.* 2019). For example, multi-cropping and crop rotations can effectively enhance biodiversity and the provision of key ecosystem services, such as pollination (Carvalheiro *et al.* 2012, Kremen & Miles 2012) and pest control (Karp *et al.* 2013, Gurr *et al.* 2016). Nonetheless, the effects are spatially variable and were found to be stronger at local than wider spatial scales, in more complex compared to simple landscapes (Lichtenberg *et al.* 2017). For example, AES participation across England did not significantly predict an increase in pollination at the national scale, though localised enhancement was observed, particularly in the late season (Image *et al.* 2022). The increase in ecosystem functionality should increase productivity of agricultural systems and indeed, it has been demonstrated to enhance (Pywell *et al.* 2015, Gurr *et al.* 2016) and stabilise (Gaudin *et al.* 2015) yields. Similarly, diversification of practices to promote ecosystem services reduced the yield gaps between organic and conventional farming (Ponisio *et al.* 2015), whilst diversified conventional farms had even higher yields than conventional farms solely relying on agrochemical inputs (Davis *et al.* 2012). Nonetheless, the impacts of diversification practices on yield can be inconsistent and increase with the quality of semi-natural habitat provision (e.g. flower strip diversity), which may increase with age (Albrecht *et al.* 2020). Moreover, the profitability of agricultural systems is important and determines the likelihood of practice uptake, and in a review, Rosa-Schleich *et al.* (2019) found that although diversified farming practices enhanced both biodiversity and associated ecosystem services, the ecological benefits for the farmer were insufficient to outbalance the economic costs of diversification practices in the short term.

Whilst promotion of diversified farming approaches with the aim of enhancing yields through ecosystem services is a strong argument in favour of biodiversity conservation, this approach alone is not enough to deliver all biodiversity conservation goals. This is because a small subset of species can deliver the necessary ecosystem services, making the other species ecologically redundant (Kleijn *et al.* 2015) and ‘not worth’ conserving. Equally, some biodiversity contributes disservices that reduce productivity (e.g. Pejchar *et al.*, 2018), which can almost fully dissipate yields in extreme cases (Kross *et al.* 2012). This means that; (i) more research is necessary to understand how much, where and under what landscape conditions, semi-natural habitats within agricultural landscapes deliver net-benefits to production (Berger *et al.* 2023); (ii) research is needed to test how effective biodiversity-friendly practices are at enhancing diversity and abundance of *all* species at landscape, and not just local scales; and (iii) ‘spared’ land may still be essential for the conservation of species incompatible with agriculture, and research should inform where and how much is needed to achieve ‘multifunctional’ and connected landscapes (Grass *et al.* 2019).

1.5. Reconciling agriculture with biodiversity

The policy framework to deliver ‘*multifunctional landscapes’* that support human livelihoods and safeguard biodiversity is mostly in place. Internationally, ambitious targets for halting, and reversing, biodiversity declines, whilst enhancing ecosystem multifunctionality have been proposed (Keping 2023). For example, the Kunming-Montreal Global Biodiversity Framework (Keping 2023), which 188 countries committed to, sets outcome goals for 2050, including:

> *‘resilience of all ecosystems are maintained, enhanced, or restored’* [Goal A], and

> '*biodiversity is sustainably used and managed and nature's contributions to people, including ecosystem functions and services, are valued, maintained and enhanced'* [Goal B].

The framework also lists targets that need to be actioned immediately and completed by 2030 in to order to achieve the goals, and these include:

> 'at *least 30 per cent of [land] are under effective restoration…'* [Target 2] and *'… are effectively conserved and managed…'* [Target 3];
>
> '*urgent management actions to halt human induced extinction of known threatened species'* [Target 4];
>
> *'areas under agriculture (…) are managed sustainably, in particular through the sustainable use of biodiversity, including through a substantial increase of the application of biodiversity friendly practices, such as sustainable intensification'* [Target 10], and
>
> '*maintain and enhance nature's contributions to people, including ecosystem functions and services'* [Target 11].

Biodiversity loss, as well as of other linked environmental issues such as climate change, have entered the mainstream of the society, meaning that biodiversity loss is no longer just an environmental issue, but also a cultural, economic, developmental and a moral one (Pullin & Knight 2009, Roe 2019). The level of *'environmental citizenship'* is rising, especially in younger generations, and is driving a societal shift towards a preference, and willingness to pay more, for sustainable and nature-friendly products (Pullin & Knight 2009, Casalegno *et al.* 2022, Gomes *et al.* 2023). For instance, within the European Union, the sales of organic products have increased by 124% between 2009 and 2019 alone (European Commission 2023). For this societal support to be maintained into the future, and for the ambitious policy targets to be delivered, there is an urgent need to demonstrate whether biodiversity-friendly management prescriptions work and to invest in evidence-based conservation and management of agricultural landscapes.

1.6. Thesis aims

Agroecological research has taught us that further agricultural expansion is incompatible with biodiversity conservation, and the ecosystem degradation arising from agricultural intensification is not sustainable. This means that we must rethink how we manage our landscapes to maximise their ability to support nature and enhance the delivery of ecosystem services that benefit people. This requires a move away from the dichotomous thinking of land-sparing *versus* sharing, or indeed organic *versus* non-organic management, and instead, evidence-based approaches, such as ecological intensification, should be incorporated into the management of agricultural landscapes. Whilst the last century has seen a substantial increase in the availability of evidence to inform biodiversity-friendly management within agricultural systems (Sutherland *et al.* 2021), there are still research gaps. Firstly, there remain major gaps in research into how agricultural practices may affect production and biodiversity in the Global South, especially when it comes to fruit production (van der Meer *et al.* 2020). Secondly, the decades of agroecological research have shown that results cannot be generalised across taxa (e.g. Bailey *et al.* 2010, Hall *et al.* 2022), nor across spatial and temporal scales (e.g. Chaplin-Kramer *et al.* 2011, 2013), and that the relationship between diversity and ecosystem service provision is also complex and variable (e.g. Karp *et al.* 2018). Very few studies consider the roles of practices or semi-natural habitats at multiple-scales (Chaplin-Kramer *et al.* 2019), and rarely do studies measure the impact of biodiversity on yield, and rather infer ecosystem services and production benefits from abundance data or presence of habitats deemed suitable (Kleijn *et al.* 2019), which is less relevant and convincing to farmers (Pywell *et al.* 2015, Gurr *et al.* 2016, Albrecht *et al.* 2020). To address some of these research gaps, the **aims of this thesis are to: (i) quantify the relative importance of landscape complexity and on-farm management practices in explaining multi-taxa biodiversity**

patterns, and (ii) by measuring ecosystem services and disservices associated with on-farm biodiversity, to inform how, where and when, biodiversity could be conserved within, and contribute to the functioning of, high-yielding agricultural landscapes. To further address the geographical gaps in agroecological knowledge (Paiola *et al.* 2020, van der Meer *et al.* 2020) and reflect the varying patterns of agricultural expansion and intensification across the globe (Newbold *et al.* 2015), **this thesis' aims are addressed across two contrasting crop systems that reflect the agricultural threats characterising the Global North and South**. The objective of this research is to inform what types of management approaches and diversification practices could support biodiversity in actively expanding and intensifying perennial fruit crop landscapes.

1.6.1. Fruticulture in north-eastern Brazil

The highest rates of agricultural intensification and expansion are predicted in South America (Laurance *et al.* 2014, Potapov *et al.* 2022), where biodiversity is predicted to suffer the most because of further agricultural development (Zabel *et al.* 2019). Brazil is in the top ten exporters of crops worldwide (FAO 2019), and the dry tropical biome of Caatinga in Brazil is an example of a region that is experiencing dual expansion and intensification, where the construction of a dam on the São Fransisco River Valley in the 1980s, gave rise to irrigated fruticulture, which has had positive socio-economic implications for the region including poverty reduction (Ferreira *et al.* 2020). Just between 1985 and 1995, the area of grapes harvested in the region increased by more than 90 times (Selwyn, 2010), whilst between 1985-2018, the area of native Caatinga vegetation decreased by 20%, mostly around agricultural areas (Salazar *et al.* 2021), and Caatinga is now undergoing a faster rate of deforestation than tropical rainforests (Dias *et al.* 2016). This is a serious threat to the wider biodiversity as the Caatinga biome is the largest semi-arid tropical forest globally and is one of the world's most biodiverse tropical drylands, harbouring over 2,000 species of plants and vertebrates with rates of endemism ranging between 7-57% across taxa (Da Silva *et al.* 2017, Araujo *et al.* 2022).

This part of the project was conducted through the Sustainable Fruit Farming in the Caatinga (SUFICA) project, which is an international collaboration between researchers, stakeholders and farmers aiming to test, through Before-After Control-Impact experiments, the effectiveness of nature-based practices at supporting ecological intensification. The goal of the SUFICA project is to enhance the sustainability and long-term resilience of fruit farming in north-eastern Brazil as it intensifies for export fruticulture. In the first part of my PhD, I worked across SUFICA project farms, and my aim was to quantify the responses of bird communities to fruticulture expansion, which also provided the 'before' data for testing the effectiveness of ecological intensification approaches [installation of perches for birds of prey, aiming to decrease crop damage (following Peisley *et al.* 2017), and the effect of cover crops on bird communities]. The COVID-19 pandemic prevented the continuation of my research in Brazil, partially due to international travel restrictions and because farmers faced a multitude of challenges, which caused them to change management priorities on their farms.

1.6.2. Viticulture in the United Kingdom

Viticulture (planting of grapevines *Vitis vinifera*) is one of the oldest and most profitable forms of agriculture of 'luxurious', rather than staple goods, and it covers about 7.3 million hectares worldwide (representing 1.8% of world's agricultural land, and 6.3% of non-feed crop area), whilst in Europe, vineyards cover 3.3 million hectares (3% of Europe's agricultural land; OIV 2023, Ritchie & Roser 2023). The majority (50-75%) of grown grapes are used to make wine, whilst up to a third are used as table grapes (Venkitasamy *et al.* 2019). Grapevines are climate sensitive (Llanaj & McGregor 2022) and recent climatic changes are increasing the climatic suitability of regions that used to be too cold for viticulture, such as the United Kingdom (UK), where summer temperatures have risen by 0.8-1 degree Celsius since 1960s, which is faster than the global average of 0.28 degree Celsius (Nesbitt *et al.* 2016, 2022, Madge 2021, Biss & Ellis 2022). Southern parts of England and Wales are now characterised by climatic conditions comparable to those in the

Champagne regions of France (Nesbitt *et al.* 2016). This has led to the viticultural industry being the fastest growing agricultural sector in the UK (Nesbitt *et al.* 2019), with the hectarage of vines across the UK quadrupling since 2000, and rapid increases in the number of wine bottles produced each year (WineGB 2022; Figure 1.1).

European vineyards have been experiencing intensification in the recent decades, and there has been a shift away from low-input practices, that saw vineyards form important parts of cultural and historical landscapes (Paiola *et al.* 2020). These shifts are happening at different rates and so across the industry, vineyards are characterised by contrasting management patterns, ranging from high-input and intensively managed dense plantations to pastoral and family-run systems that are managed by a combination of approaches including abiding to biodynamic principles (Döring *et al.* 2015, Winter *et al.* 2018, Paiola *et al.* 2020). This is also characteristic of the UK wine industry, which has got a strong focus on sustainability with its own sustainability scheme 'Sustainable Wines of Great Britain' (hereafter 'SWGB'). The scheme strives to ensure environmental, social, economic sustainability within the industry, through a process of continual improvement (WineGB 2022), and to date, over 80 vineyards, accounting for over 55% of the hectarage are members of SWGB (WineGB 2022). 'Sustainable' management under the scheme is vaguely defined, which creates a gradient of management approaches across the industry. European, and indeed UK, vineyard landscapes are on their way to becoming *multifunctional landscapes*, as unlike most other agricultural systems, they hold strong cultural significance and are linked to the tourism industry (Sussex Modern 2023), through vineyard tours and tasting events. Agroecological research within the UK wine industry is timely for informing the development of the industry and its sustainability scheme, and this provides an exciting opportunity to study the wider benefits that biodiversity could bring across these landscapes, and how and where biodiversity could be incorporated to support crop production and wider wellbeing.

1.7. Thesis structure

The work presented in this thesis is the result of project changes arising from disruption caused by the COVID-19 pandemic, which prevented the continuation of fieldwork across the SUFICA project farms in Brazil post-March 2020. In **Chapter 2,** I present the results of a single fieldwork season across the grape and mango farms in north-eastern Brazil, where I compare the bird community composition between the remnant Caatinga forest and fruit farm patches. Specifically, I consider how the responses to agricultural expansion and the resulting habitat loss vary based on species' traits (diet and habit associations, and conservation status).

In late 2020, I set up a new research project across UK vineyards, and I describe the study site selection process in **Chapter 3**. The objective of the site selection was to maximise the landscape complexity and vineyard management gradients, whilst choosing sites that are representative of the broader industry to be able to test the relative effects of environmental and management variables on biodiversity, and deliver industry-specific recommendations. Hence, in **Chapter 4,** I examine the relative impact of surrounding landscape complexity, semi-natural habitat features and vineyard management practices on bird and arthropod biodiversity, and I compare biodiversity between vineyards under different management regimes (organic *versus* non-organic, and based on accreditation through an industry-specific sustainability scheme).

Bird communities inhabiting farm systems can both benefit and harm production through the provision of ecosystem services and disservices (Pejchar *et al.* 2018), and I explore the net effects of birds to viticulture in **Chapter 5**. In this chapter, I present the results of an exclusion experiment and of grape damage assessments, and I explore the spatial and temporal variation in grape damage, relating it to the abundance of key ecosystem service and disservice providing species. I then relate grape damage rates to yield and consider the relative effects of farm management and vineyard configuration on yield.

Biodiversity contributions within agroecosystems stretch beyond those directly affecting crop production, as agricultural areas, particularly vineyards, hold cultural significance within societies. Additionally, there is growing demand for testing emerging technologies, such as passive acoustic monitoring, for monitoring biodiversity (Cardinale *et al.* 2012). I combine these two concepts in **Chapter 6,** where I firstly characterise vineyard soundscapes using acoustic indices and relate them to bird biodiversity, described in Chapter 4. Secondly, I relate the acoustic indices to visitors' experience of vineyard tours, as measured through a questionnaire, and thirdly, I explore the impact of experimental soundscape enhancement on the visitors' experience. I use the results to argue that soundscapes should be considered, and conserved, within multifunctional landscapes.

Finally, in **Chapter 7**, I provide a synthesis of the results described throughout the thesis and draw some general conclusions.

All chapters are written as standalone pieces of work with separate figures, reference lists and supporting materials presented at the end of each chapter. **Chapters 2, 4-6** are written in the style of scientific papers and under '**List of publications'**, I indicate how far along the publishing process each chapter is. Despite not being able to continue my own work across the SUFICA farms, I remained involved with the SUFICA project and have co-authored several publications, which are outlined in **Appendix 1**.

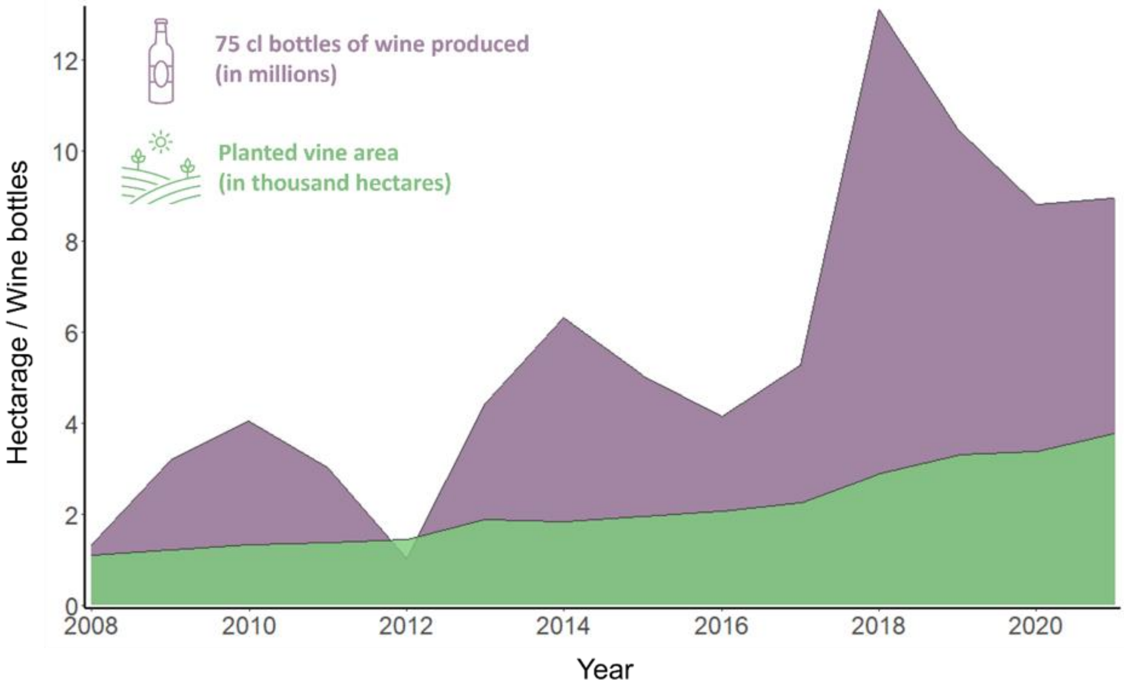

Figure 1.1. The total area, in thousand hectares of commercial vineyards planted (green), and the number of wine bottles (purple), in millions, produced by wineries across the UK between 2008 and 2022. Data were from EnglishWine.com, compiled by Stephen Skelton, and accurate in March 2022.

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Appendix 1 - List of co-authored publications arising from my involvement in the SUFICA project

Salazar, A.A., Arellano, E.C., Muñoz-Sáez, A., Miranda, M.D., Oliveira da Silva, F., **Zielonka, N.B.,** Crowther, L.P., Silva-Ferreira, V., Oliveira-Reboucas, P. & Dicks, L.V. 2021. *Restoration and Conservation of Priority Areas of Caatinga's Semi-Arid Forest Remnants Can Support Connectivity within an Agricultural Landscape.* Land 10: 550. https://doi.org/10.3390/land10060550.

I took on a supporting role in the conceptualisation and validation of the analytical approaches, gathering of resources and in writing and editing the manuscript.

Oliveira da Silva , F., Arellano, E.C., Felipe Viana , B.; Silva-Ferreira, V., Oliveira-Reboucas , P., Rojas , N/, Muñoz-Sáez, A., Jimenez , V.P., **Zielonka, N.,** Crowther, L. & Dicks, L.V.. *Co-production of agroecological innovations to enhance sustainability in South American fruit farms*. People and Nature *[revision submitted to People and Nature].*

This work describes the ecological intensification approaches that were tested by the SUFICA project, including the provision of perches for birds of prey, which I designed and worked with the farmers and co-authors to implement across the farms. A protocol that I wrote for ad-hoc monitoring of the use of the perches by the farmers contributed to this published work. I also provided comments on this manuscript.

Crowther, L.P., Luke, S.H., Arellano, E.C., McCormack, C.G., Ferreira, V., Hillier, J., Heathcote, R., Kloen, H., Muñoz-Sáez, A., Oliveira-Rebouças, P., Oliveira da Silva, F., Rojas-Arévalo, N., **Zielonka, N. &** Dicks, L.V. *The Cool Farm Biodiversity metric: an evidence-based online tool to report and improve management of biodiversity at farm scale.* Ecological Indicators *[under review].*

I contributed to the scoring of conservation actions for the Mediterranean and semi-arid biome and provided comments on this manuscript.

Chapter 2: Distinct bird communities in fruit farm and forest patches across intensively managed fruit farm landscapes in the semi-arid Caatinga biome in north-eastern Brazil.

© Natalia Zielonka: Table grape field (top) and Picui ground dove *Columbina picui* nestlings, Brazil.

Natalia B. Zielonka, Eduardo Arellano[2,3], Liam P. Crowther[4], Vinina Ferreira[5], Andrés Muñoz-Sáez[6], Patricia Oliveira-Rebouças[7], Fabiana Oliveira da Silva[8], Simon J. Butler[1*] & Lynn V. Dicks[1,9*]

[1] School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[2] Instituto para el Desarrollo Sustentable & Facultad de Agronomía y Sistemas Naturales, Pontificia Universidad Católica de Chile, Santiago 7830436, Chile
[3] Center of Applied Ecology and Sustainability (CAPES) Santiago 7820244,
[4] School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
[5] Universidade Federal do Vale do São Francisco, Petrolina, PE, 56300-990, UNIVASF, Brazil[6]
[6] Facultad de Ciencias Agronómicas, Universidad de Chile, Santiago, Chile 8820808
[7] Departamento de Tecnologia e Ciências Sociais, Universidade do Estado da Bahia - Campus III (UNEB) Juazeiro, 48904-711, Brazil
[8] Universidade Federal de Sergipe, 49680-000, Nossa Senhora da Glória, Sergipe, Brazil / National Institute of Science and Technology in Interdisciplinary and Transdisciplinary Studies in Ecology and Evolution - INCT-IN-TREE
[9] Department of Zoology, University of Cambridge, CB2 3EJ, UK.

** Joint last authors*

Acknowledgments

We thank our study farms and farm managers for access to field sites and support with in-field logistics. We thank Gilson Amorim and Danilo Soares De Souza for their assistance in fieldwork. We thank Prof Zhijun Ma and an anonymous reviewer for their comments on this manuscript, and the handling editor, Prof Jeremy Wilson. This research was funded by: NBZ was supported by UKRI Biotechnology and Biological Sciences Research Council Norwich Research Park Biosciences Doctoral Training Partnership [Grant number BB/M011216/1], and other co-authors were funded through the Nexus project initiative from Newton Fund/BBSRC (BB/R016429/1) and ANID project NEXUS (BB/R0164291), and Center of Applied Ecology and Sustainability (CAPES) (PIA/BASAL FB0002).

Abstract

(English)

Agricultural expansion and intensification drive changes in bird assemblages and contribute to the homogenisation of communities. This study is the first to describe the bird communities across intensively managed fruit farms in the semi-arid biome of Caatinga in north-eastern Brazil. We show that fruit farm patches host 56% lower bird abundance and 61% lower species richness compared to the remnant Caatinga forest fragments. Bird communities within the fruit farms were distinct from those within the forest patches, and they were characterised by species with broader niches, including two non-native species.

(Brazilian Portuguese)

A expansão e a intensificação da agricultura modificam as comunidades de aves e contribuem para a sua homogeneização. Este estudo é o primeiro a descrever as comunidades de aves em fazendas de fruticultura com manejo intensivo situadas no bioma Caatinga, na região semiárida do Nordeste do Brasil. Nós mostramos que as manchas no interior das fazendas possuem menor abundância (56%) e riqueza (61%) em comparação com os fragmentos remanescentes da floresta de Caatinga. As comunidades de aves no interior das fazendas de fruticultura diferiram daquelas presentes nos fragmentos de floresta, e se caracterizaram por espécies com nichos ecológicos mais amplos, incluindo duas espécies exóticas.

2.1. Introduction

Agricultural landscapes occupy the largest part of world's terrestrial surface (Foley *et al.* 2005), and land use change due to agricultural expansion and intensification is a major cause of biodiversity loss globally (Newbold *et al.* 2016, Jaureguiberry *et al.* 2022). Agriculture is still rapidly expanding in parts of the world, a trend that is predicted to persist over the coming decades (Godfray *et al.* 2010). The highest rates of agricultural expansion are predicted in the Southern Hemisphere, including South America (Zabel *et al.* 2019), and threaten many of world's biodiversity hotspots (Molotoks *et al.* 2018). The responses of biodiversity to agriculture in these regions remain largely unstudied (van der Meer *et al.* 2020).

Intensively managed agricultural landscapes are frequently homogeneous and experience high levels of anthropogenic disturbance, thus only species able to adapt to these conditions persist (Tscharntke *et al.* 2012, Newbold *et al.* 2013, Silva *et al.* 2021). Habitat and diet generalists migratory and short-lived species do better within human-modified habitats, at the expense of species with narrower niches (Blackburn *et al.* 2009, Newbold *et al.* 2013, Val *et al.* 2018, Smith *et al.* 2019). This can lead to homogenisation of assemblages within agricultural landscapes and could result in the wider homogenisation of global biodiversity under agricultural expansion and intensification scenarios (Pereira *et al.* 2012). Retaining habitat heterogeneity across agricultural landscapes can counteract this by supporting more diverse communities (Benton *et al.* 2003, Martin *et al.* 2019, Sasaki *et al.* 2020). Within fragmented agricultural landscapes, edge habitats are particularly important as they harbour more biodiversity (Martin *et al.* 2019, Sasaki *et al.* 2020), and retaining high edge density has been shown to improve connectivity and promote more diverse assemblages (Boesing *et al.* 2018, Silva *et al.* 2020). This in turn increases the resilience of agricultural habitats to change and supports the provision of ecosystem services (Tscharntke *et al.* 2005, Karp *et al.* 2018, Redhead *et al.* 2020).

Human-modified and disturbed habitats facilitate the spread and establishment of non-native species, a pattern well documented in mammals (Doherty *et al.* 2016, Hradsky *et al.* 2017), birds (Bonter *et al.* 2010, Colléony & Shwartz 2020, Shivambu *et al.* 2020) and plants (Taylor & Irwin 2004). Traits that predict occurrence in human-modified landscapes are common among non-native species (e.g. large body size, low-level of specialism; Blackburn *et al.* 2009), and thus the proportion of communities that non-native species make up increases with intensity of land-use (Sofaer *et al.* 2020). This is of conservation concern as invasive species threaten native species through competition, predation and disease spread, and can drive native populations to extinction (Bellard *et al.* 2016, Blackburn *et al.* 2019).

The Caatinga biome in Brazil is the largest semi-arid tropical forest globally and is one of the world's most biodiverse tropical drylands, harbouring over 2,000 species of plants and vertebrates (Da Silva *et al.* 2017, Araujo *et al.* 2022). The Caatinga has a rich bird assemblage of 548 species, representing almost 29% of Brazilian species, with 67 species that are endemic or near-endemic to Caatinga (Araujo & Da Silva 2017, Araujo *et al.* 2022). Endemic birds in the Caatinga have already been shown to be vulnerable to climate changes (Gonçalves *et al.* 2023), as many are diet and habitat specialists (Araujo & Da Silva 2017, Vale *et al.* 2018). The Brazilian Caatinga is undergoing a faster rate of deforestation than tropical rainforests (Miles *et al.* 2006, Dias *et al.* 2016) and has experienced high levels of anthropogenic disturbance (Teixeira *et al.* 2021). The Caatinga is Brazil's second most degraded biome, with half its original area already lost and only 1% of the remaining Caatinga under strict legal protection (Antongiovanni *et al.* 2020, Teixeira *et al.* 2021). Over the past three decades, much of the disturbance and land-use change has resulted from irrigated fruit farming, which is concentrated around the São Francisco River Valley (de Espindola *et al.* 2021, Salazar *et al.* 2021, Jardim *et al.* 2022).

We studied the bird communities inhabiting table grape and mango farms around Petrolina, in the São Francisco River Valley. Our objectives were to provide the first description of bird communities across these fruit farms, comparing the communities inhabiting the fruit farms and nearby remnant Caatinga forest fragments. We predicted that (1) bird assemblages would be more diverse within Caatinga forest habitat patches, and (2) that a higher proportion of the fruit farm communities would be made up of habitat generalists, whilst species with narrower niches would be limited to the Caatinga forest.

2.2. Materials and methods

2.2.1. Study area

We studied bird communities across 10 irrigated fruit farms (three grape and mango, seven grape-only) in north-eastern Brazil (9.41°S, 40.50°W; Figure 2.1). Farms were at least 5 km apart (max 84 km) and they varied in size of production area (mean: 198.7 ha, range 13.55 – 520.3 ha). All farms were intensively managed for export agriculture and relied heavily on agrochemicals.

The study area is characterised by the semi-arid biome of Caatinga, which has a stable but hot climate and distinct dry (May-December) and wet (January-April, >70% annual rainfall; Jardim *et al.* 2022) seasons. The native vegetation of the Caatinga biome is a mosaic of dry arboreal and shrub forests, and open, rocky areas (Leal *et al.* 2005, Da Silva *et al.* 2017). In the dry season, forests and shrubs are mostly bare and green foliage is limited to the wet season (Leal *et al.* 2005). Due to ongoing habitat degradation, particularly around agricultural areas, Caatinga is becoming increasingly less dense with more open areas (Ribeiro *et al.* 2015, Antongiovanni *et al.* 2020).

2.2.2. Bird surveys

We used 10-minute point counts to survey birds during the wet season between January-March 2020. We performed surveys in two habitat types, 'Caatinga forest' and 'fruit farms', which could be grape or mango farm parcels. Depending on farm size and Caatinga availability, we conducted surveys at 1-3 locations per habitat type per farm, totalling 56 survey locations (n=26 fruit farm locations across 10 farms, of which 17 were in grape and 9 in mango parcels; and n=20 Caatinga forest locations across seven farms). All surveys within a farm were performed on the same day, and we surveyed each location twice during the wet season (mean: 11.8 days between surveys; range: 10-14). All survey sites were at least 50 m from the edge of the surveyed habitat patch and any roads, at least 150 m away from other survey locations within the same habitat patch (mean within a farm: 312 m; range: 152-583 m), and at least 250 m away from survey locations in the other habitat patch (mean within a farm: 457 m; 257-891 m). Surveys were conducted by one observer between 06:00-11:00, only in fair weather conditions, and all seen and heard species within a 50 m radius were recorded, excluding birds that were flying over.

2.2.3. Variables

Our sites spanned a landscape complexity gradient (Figure 2.1), and we quantified landscape composition within a buffer with a 2.5 km radius around a central point of each study farm. Within each buffer, we calculated the proportion cover by: Caatinga forest, agriculture, urban areas, and water (30 m vector land cover maps; MapBiomas 2018), using ArcGIS 10.6. (ESRI 2018). We also quantified the total edge length using FRAGSTATS 4.2 (McGarigal 1995). We checked the predictors for collinearity, and found a strong, negative correlation between *Caatinga cover* and *Agriculture cover* (Spearman's rho = 0.789, df = 9, t-value = 8.756, p-value < 0.001), thus, proceeded to use *Caatinga cover* only in analyses. We did not consider cover by water and urban areas in our analyses as these only featured in up to 2 landscapes.

We collated information on the diet, habitat associations and species' adaptability potential for the recorded bird species (see Supplementary Materials Table S2.1). Firstly, we characterised the species by their primary diet (*omnivore, insectivore, granivore, carnivore, frugivore, scavenger and nectarivore;* Billerman *et al.* 2022). We only recorded a single species of scavenger and nectarivore, so we excluded these from trait-based analyses. Secondly, we grouped the species based on their adaptability to anthropogenic habitats and disturbance according to Araujo & Da Silva 2017. The three adaptability categories were '*high adaptability*' (species commonly present in human-modified habitats), *'medium adaptability',* and *'low adaptability'* (species only present in intact and almost undisturbed habitats). These adaptability categories were closely related to the species' habitat use in our study: species with high and medium adaptability were exclusively open-area or generalist species, whereas all low adaptability species were forest species that relied on Caatinga forest. Lastly, we classified species based on their distribution, either as *endemic* if the species was exclusively, or near-exclusively found in the Caatinga biome (Araujo & Da Silva 2017), or as *non-native* if the species was not native to Brazil, and classified the remaining species as *other*.

2.2.4. Statistical analyses

We used Non-metric Multidimensional Scaling (NMDS) using Bray-Curtis dissimilarity (following Clarke *et al.* 2014) to compare the bird communities between the surveyed habitat patches (mango and grape farms, and Caatinga forest). To compare bird communities between habitat patches, we used permutational analysis of variance (PERMANOVA) with 999 permutations (Anderson 2001). This was performed in the *VEGAN* package (Oksanen 2010).

We calculated bird abundance, species richness and Shannon diversity per survey and related these to landscape and local habitat predictors in linear mixed-effect models, using the *lme4* package (Bates *et al.* 2015). The predictors were *Habitat* (two levels after combining mango and grape farms to *fruit farms*), *Caatinga cover* (proportion cover by Caatinga forest within 2.5 km buffer), *Edge density* (the total length of edges within 2.5 km buffer), and an interaction *Caatinga cover*Habitat,* with survey ID nested in Farm ID fitted as a random effect. We fitted Gaussian models with log link function for abundance and species richness, and inverse link function for Shannon diversity.

We proceeded with full models, accepting predictor significance based on whether the model estimates with 95% confidence intervals included zero, and if $p < 0.05$. We inspected the distribution of residuals, dispersion and checked for influential points using the *DHARMa* package (Hartig 2022). All analyses were performed in R 4.2.0 (R Core Team 2021).

To understand which bird traits affected the likelihood of species occurrence in the surveyed fruit farm and Caatinga forest patches, we used paired t-tests to compare (fruit farm *vs.* Caatinga forest) the number of individuals of bird species belonging to each of five dietary groups, three groups defining species' adaptability to human-modified habitats, and species that were either endemic or non-native to the Caatinga biome. We were only able to perform these tests for seven of the 10 farms (n=98 surveys), where we surveyed both fruit farm and Caatinga forest habitat patches.

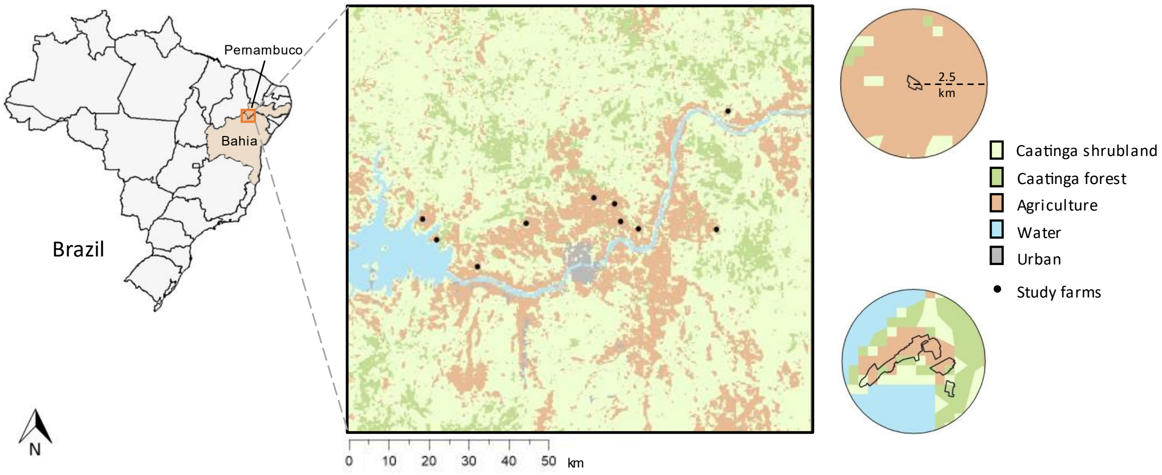

Figure 2.1. Study area in the states of Pernambuco and Bahia in the Caatinga, north-eastern Brazil. Bird communities at 10 grape and mango farms (black dots) were studied and related to the landscape in a 2.5 km radius buffer around each farm. Two circular buffers (2.5 km radius) are shown, presenting the most homogenous (top) and most heterogenous (bottom) landscape.

2.3. Results

Across 114 surveys, we recorded 2,125 individuals belonging to 78 species (see Supporting Online Information table S1). We recorded 66 species in the Caatinga forest (including 27 Caatinga forest-exclusive species; 971 individuals), 28 species in mango farms (2 mango farm-exclusive species; 311 individuals) and 47 species in grape farms (6 grape farm-exclusive species; 843 individuals). The six most abundant species within the fruit farm patches made up 57% of all individuals recorded within the farms, and these species were: *Columbina picui, Sporophila albogularis* (endemic)*, Volatinia jacaria, Paroaria dominicana* (endemic)*, Estrilda astrild* (non-native)*, Passer domesticus* (non-native). *Columbina picui* was also the most abundant bird within Caatinga forest surveys, followed by *Cathertes aura, Guira guira, Voatinia jacarina, Pitangus sulphuratus, Zenaida auriculata*. The NDMS showed that bird communities in the fruit farms differed significantly from those within Caatinga patches (PERMANOVA: $R^2 = 0.439$, $p < 0.001$), but there was little difference in the bird communities between grape and mango farms (Figure 2.2), thus we combined the fruit farm patches surveys for subsequent analyses.

Average bird abundance (Caatinga forest: 24.3 ± 1.25, fruit farms: 15.6 ± 0.57 SE), species richness (Caatinga forest: 11.3 ± 0.36, fruit farms: 7.01 ± 0.25) and Shannon diversity (Caatinga forest: 2.18 ± 0.04, fruit farms: 1.77 ± 0.04) per point count were significantly higher in the Caatinga forest patches than in fruit farms (Table 2.1). Bird abundance and diversity were not affected by the proportion of Caatinga cover, nor edge density in the landscape surrounding the farms (Table 2.1).

Omnivorous species were most common (40% of species and 61% of total abundance), and were equally likely to occur in the Caatinga forest and fruit farm habitat patches ($t(6) = -0.422$, $p = 0.688$; Figure 2.3a). The abundance of insectivorous (n=27 species; $t(6) = 5.605$, p-value = 0.001; Figure 2.3b) and frugivorous species (n=5 species; $t(6) = 3.07$, p-value = 0.022; Figure 2.3c) was significantly higher in the Caatinga forest than in the fruit farm patches. The abundance of granivorous (n=4; t(6) = -1.245, p-value = 0.259) and carnivorous (n=6; t(6) = 0.281, p-value = 0.788) species did not differ between the surveyed habitat patches (Figure 2.3d-e).

Most of the recorded species (58/78) were classified as having high adaptability to human-modified habitats and accounted for 74% of the total recorded individuals (897 individuals in Caatinga forest and 1,128 in fruit farms). Of the other 20 recorded species, 10 species were classed as medium adaptability (53 individuals in Caatinga forest, 22 individuals in fruit farms), and 10 were low adaptability (21 individuals in Caatinga forest, 4 individuals in fruit farms). Species of medium (t(6) = 4.032, p-value = 0.007) and low-adaptability (t(6) = 2.714, p-value = 0.035) were significantly more abundant within the Caatinga forest patches than in the fruit farms, but the abundance of high-adaptability species did not differ between the habitats (t(6) = -0.181, p = 0.863, Figure 2.3f-h).

Altogether, we recorded 10 endemic (see Supporting Online Information table S1) and 2 non-native species to the Caatinga biome. All 10 endemic species were recorded in the Caatinga forest but only 6 within the fruit farms, though the abundance of endemic species did not vary significantly between the habitat patches (t(6) = -1.002, p-value = 0.355, Figure 2.3i). The two non-native species were Common Waxbill *Estrilda astrild* (80 total sightings of which 77 were in fruit farms) and House Sparrow *Passer domesticus* (53 total sightings, and only recorded in fruit farms), and the number of non-native species individuals was significantly higher in fruit farms (130/133, 98%) than Caatinga forest patches (t(6) = -4.785, p = 0.003, Figure 2.3j).

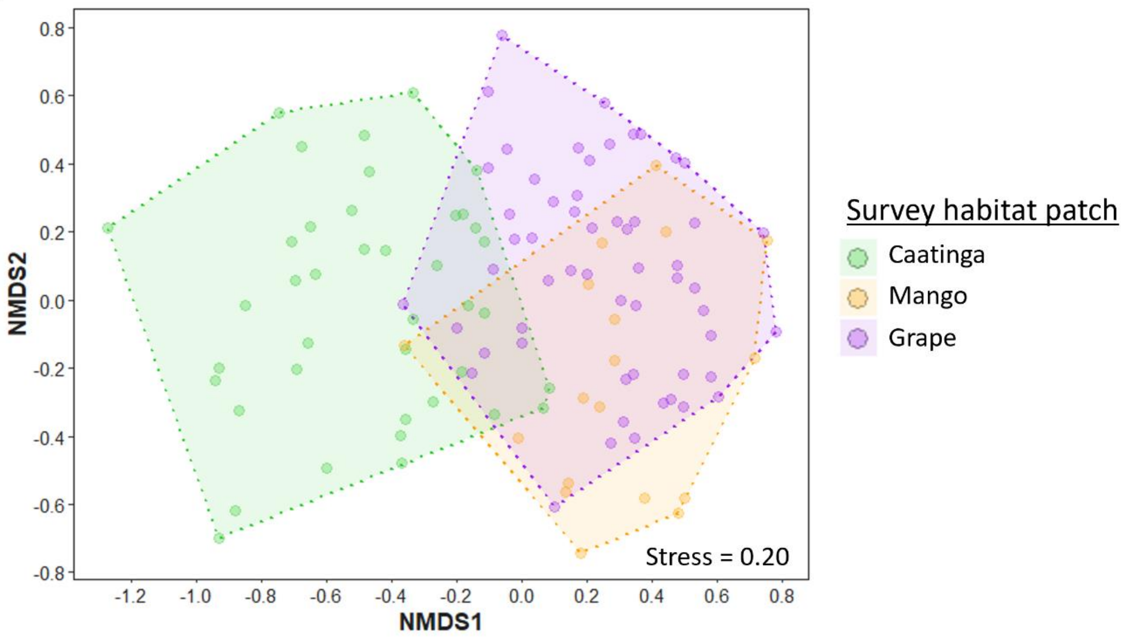

Figure 2.2. Non-metric multidimensional (NMDS) scaling of the abundance and composition of bird communities considering individual species across fruit farm and remnant Caatinga forest patches. Coloured points represent survey sites (n=114) in each habitat patch, and the minimum convex polygons group these according to the survey habitat patch.

Table 2.1. Model outputs from general linear mixed models testing the effects of survey habitat, proportion of Caatinga cover and edge density in a 2.5 km buffer around study fruit farms on bird abundance, raw species richness and Shannon diversity (n=114 surveys). Survey ID (n=57) nested in Farm ID (n=10) was fitted as a random effect. The model estimates with 95% confidence intervals (CI), t-value, p-value and model AIC and R2 values are reported.

	Variable	Estimate (95% CI)	t-value	p-value	R2	AIC
Abundance	Intercept (Caatinga forest)	2.061 (-4.759; 8.880)	0.592	0.555	0.316	81.85
	Fruit farm	-0.431 (-0.786; -0.076)	-2.374	0.019		
	Caatinga cover	0.003 (-0.004; 0.010)	0.903	0.368		
	Edge density	0.141 (-0.877; 1.158)	0.271	0.787		
	Habitat patch * Caatinga cover	0.0002 (-0.008; 0.008)	0.052	0.959		
Species richness	Intercept (Caatinga forest)	4.537 (-0.273; 9.198)	1.887	0.062	0.484	145.25
	Fruit farm	-0.440 (-0.679; -0.198)	-3.528	<0.001		
	Caatinga cover	0.002 (-0.002; 0.006)	1.042	0.300		
	Edge density	-0.327 (-1.025; 0.391)	-0.91	0.365		
	Habitat patch * Caatinga cover	-0.0006 (-0.006; 0.005)	-0.203	0.840		
Shannon diversity	Intercept (Caatinga forest)	4.356 (-1.682; 1.355)	1.383	0.170	0.303	59.187
	Fruit farm	-0.456 (0.042; 0.196)	-2.779	0.006		
	Caatinga cover	0.0003 (-0.001; 0.001)	0.092	0.927		
	Edge density	-0.325 (-0.133; 0.320)	-0.692	0.491		
	Habitat patch * Caatinga cover	0.002 (-0.002; 0.001)	0.425	0.672		

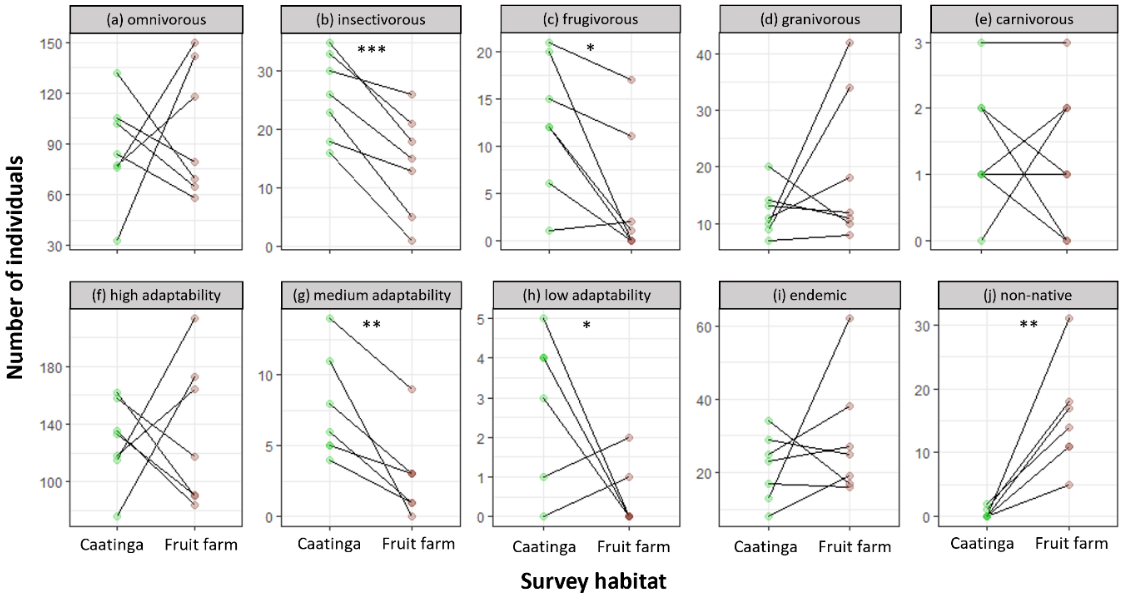

Figure 2.3. Number of individuals of bird species belonging to one of the five dietary groups (a-e), three groups defining species' adaptability ability to human-modified habitats (f-h), and species that are endemic to the Caatinga biome (i) or non-native to Brazil (j), as recorded in Caatinga forest (n=40) and fruit farm (n=58) habitat patches across 7 study farms. Significant differences, as tested by paired t-tests, are indicated by asterisks as follows: * $p < 0.05$, ** $p < 0.01$, *** $p<0.001$.

2.4. Discussion

Our study shows that fruit farming within the semi-arid biome of Caatinga in north-eastern Brazil has a strong effect on native bird communities. Overall, bird abundance, species richness and Shannon diversity within fruit farm patches were significantly lower compared to adjacent patches of remnant Caatinga forest, with a third of all species being only recorded within the forest patches. Fruit farms not only hosted fewer birds and less diverse communities, but they were also characterised by different bird assemblages, composed of species with broader niches, including two non-native species.

Habitat type was the strongest driver of bird community structure, with Caatinga forest and fruit farm patches harbouring distinct assemblages. Species' responses to agricultural expansion depend on their traits, such as the level of specialisation and dispersal ability (Tscharntke *et al.* 2012, Newbold *et al.* 2013, Silva *et al.* 2021) and, in our system, the occurrence of insectivorous and frugivorous species was significantly lower within the fruit farms. Lower abundance of insectivores within farms has been observed in other tropical systems (e.g. Sekercioglu 2012), and may be linked to the use of agrochemicals within farms, which likely decreases prey availability. However, the reduction in frugivorous species within fruit farms was unexpected, particularly as farmers frequently report birds feeding on grapes (Herrmann & Anderson 2016, Peisley *et al.* 2017). Fruit damage caused by birds is often the highest at field edges neighbouring native habitats (Peisley *et al.* 2017, Olimpi *et al.* 2020), which we did not survey, and we hypothesise that the density of frugivorous species may be higher there, particularly in fields with ripe fruits. We also only surveyed bird communities in the wet season when there was increased abundance of fruit within the Caatinga forest, and we hypothesise that the abundance of frugivorous species within farms may increase during the dry season when alternative resources are scarcer.

Across our study landscapes, 87% of the species were habitat generalists or open-habitat species, and predominantly omnivorous; five species with these traits made up over half of all bird sightings within the fruit farms. This aligns with findings from guava farms in the Caatinga biome, where omnivorous and disturbance-resistant species were most abundant (Silva *et al.* 2021). In our study, species characterised by these traits included two non-native species to Brazil: Common Waxbill and House Sparrow. These species occurred predominately within the fruit farms, the House Sparrow exclusively so, which supports the well-established pattern that human-modified habitats support invasions and persistence of non-native species (Pyšek *et al.* 2010, Smith *et al.* 2019, Colléony & Shwartz 2020, Shivambu *et al.* 2020). These species may be having a negative impact on native species by restricting their access to resources and breeding areas (Peck *et al.* 2014, Le Louarn *et al.* 2016), though as they seem limited to the fruit farm patches, their impact may be less than observed elsewhere (Blackburn *et al.* 2019).

Population declines resulting from agriculture are often more pronounced among endemic species (Newbold *et al.* 2013, Smith *et al.* 2019), though we found mixed patterns across the studied fruit farms. In line with previous literature (Newbold *et al.* 2013) and our prediction, we found that seven out of the 10 endemic species had specialised diets and these species were exclusively recorded in the Caatinga forest. However, two endemics, the White-throated seedeater *Sporophila albogularis* and Red-cowled cardinal *Paroaria dominicana,* were more abundant within fruit farms than the forest patches. These species use open habitats, and have been observed to forage and breed within guava fruit farms in the Caatinga biome (Silva *et al.* 2021), thus they are likely to persist, if not increase in abundance, under agricultural expansion in the region.

Contrary to expectations, Caatinga cover and edge density in the wider landscape did not affect bird abundance and diversity. The importance of semi-natural habitat cover and high edge density for maintaining biodiversity has been well documented within agricultural landscapes (Carrara *et* *al.* 2015), including in similar biogeographical regions (Boesing *et al.* 2017, Muñoz-Sáez *et al.* 2017, Adorno *et al.* 2021, Estupiñan-Mojica *et al.* 2022). Landscape heterogeneity and edge density support species dispersal and spill-over through decreased isolation of habitat patches (Silva *et al.* 2020, Boesing *et al.* 2021). Nonetheless, in high-contrast landscapes, limited spill-over across habitats has been noted (Boesing *et al.* 2021, Alvarez-Alvarez *et al.* 2022). Our study area is characterised by such high contrast of habitats as the Caatinga forest is seasonally dry and structurally complex, whilst the fruit farms are irrigated, planted in straight rows and experience high levels of disturbance. Furthermore, the area has experienced prolonged disturbance (da Silva *et al.* 2018), and thus, the assemblages are likely filtered with species that are more resilient to human disturbances, and less reliant on the native vegetation, persisting (Filgueiras *et al.* 2021).

2.5. Conclusion

Our study documented the effects of fruit farming on bird assemblages within the highly diverse Caatinga biome, and our findings suggest that the continuing agricultural expansion and intensification may result in the homogenisation of avian communities. As observed in other regions (Newbold *et al.* 2013, Smith *et al.* 2019, Boesing *et al.* 2021), and within the Caatinga (Silva *et al.* 2021), intensively managed fruit farms harbour more generalist species that are able to adapt to human-modified habitats. The resulting species loss is detrimental to biodiversity more widely, but can also be disadvantageous to production, as some bird species, such as insectivores, can deliver important ecosystem services including pest control (Barbaro *et al.* 2017, Boesing *et al.* 2017, Martin *et al.* 2019). This calls for conservation measures to be incorporated within farming, which can include retaining Caatinga forest fragments and patches of trees within the farms, to act as stepping stones, and to increase connectivity (Silva *et al.* 2020, Salazar *et al.* 2021). Caatinga harbours diverse communities of endemic species, many of which are habitat specialists and sensitive to habitat loss (Antongiovanni *et al.* 2020, Salazar *et al.* 2021, Estupiñan-

Mojica *et al.* 2022), and we argue that increasing the amount of Caatinga that is under strict legal protection in areas that have not experienced past disturbance is crucial to addressing the wider decline of biodiversity across the biome.

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Chapter 2 Supplementary Materials

Table S2.1. List bird species recorded across fruit farm and Caatinga forest patches in north-eastern Brazil. For each species, the number of individuals recorded per habitat patch is given, and the species' diet, habitat association, adaptive ability and conservation status in the Caatinga (section 2.2.3).

Species	Grape farm	Mango farm	Caatinga forest	Diet	Habitat association	Adaptive ability	Conservation status
Ardea cocoi	1	0	0	carnivorous	open	medium	native
Athene cunicularia	11	0	1	carnivorous	open	high	native
Bubulcus ibis	0	2	0	carnivorous	open	high	native
Cantorchilus longirostris	1	0	6	insectivorous	forest	low	endemic
Caracara plancus	3	2	1	carnivorous	open	high	native
Casiornis fuscus	1	0	0	insectivorous	forest	low	native
Cathartes aura	11	2	105	scavenger	open	high	native
Certhiaxis cinnamomeus	0	0	1	insectivorous	open	high	native
Chlorostilbon lucidus	3	0	26	nectarivorous	generalists	medium	native
Chrysomus ruficapillus	2	0	10	omnivorous	open	high	native
Coccyzus americanus	1	0	1	omnivorous	generalists	medium	native
Coccyzus melacoryphus	0	0	9	omnivorous	generalists	high	native
Coereba flaveola	0	0	4	omnivorous	generalists	high	native
Colaptes melanochloros	2	0	1	insectivorous	generalists	high	native
Columbina picui	156	69	129	omnivorous	open	high	native
Columbina talpacoti	25	24	18	omnivorous	open	high	native
Compsothraupis loricata	1	0	1	insectivorous	generalists	medium	endemic
Coragyps atratus	9	2	42	omnivorous	open	high	native
Coryphospingus pileatus	1	0	3	granivorous	generalists	high	native
Crotophaga ani	2	0	20	insectivorous	open	high	native
Cyanocorax cyanopogon	2	12	5	omnivorous	generalists	medium	native
Cyclarhis gujanensis	1	0	0	insectivorous	generalists	high	native

Dryobates passerinus	0	0	3	insectivorous	generalists	high	native
Egretta thula	1	1	0	insectivorous	open	high	native
Empidonomus varius	0	0	1	omnivorous	generalists	high	native
Estrilda astrild	38	39	3	omnivorous	open	high	non-native
Eupetomena macroura	4	0	1	frugivorous	open	high	native
Euphonia chlorotica	0	0	5	frugivorous	generalists	high	native
Eupsittula cactorum	25	0	50	frugivorous	generalists	high	endemic
Falco femoralis	0	1	0	carnivorous	open	high	native
Fluvicola nengeta	11	3	0	insectivorous	open	high	native
Formicivora melanogaster	0	0	7	insectivorous	generalists	medium	native
Forpus xanthopterygius	0	0	5	frugivorous	open	high	native
Furnarius leucopus	0	0	1	insectivorous	generalists	high	native
Gnorimopsar chopi	0	0	1	omnivorous	open	high	native
Guira guira	29	15	65	insectivorous	open	high	native
Hemitriccus margaritaceiventer	0	0	1	insectivorous	generalists	high	native
Herpetotheres cachinnans	0	0	1	carnivorous	generalists	high	native
Herpsilochmus atricapillus	0	0	1	insectivorous	forest	low	native
Herpsilochmus sellowi	0	0	1	insectivorous	generalists	medium	endemic
Hirundo rustica	2	9	0	insectivorous	open	high	native
Icterus jamacaii	0	0	14	omnivorous	generalists	high	endemic
Lepidocolaptes angustirostris	0	0	1	insectivorous	generalists	high	native
Leptotila rufaxilla	1	0	2	omnivorous	forest	low	native
Megarynchus pitangua	0	0	1	insectivorous	generalists	high	native
Mimus saturninus	3	3	6	omnivorous	open	high	native
Molothrus bonariensis	6	1	2	omnivorous	open	high	native
Myiarchus tuberculifer	0	0	1	insectivorous	forest	low	native
Myiodynastes maculatus	0	0	1	omnivorous	forest	low	native
Myiothlypis flaveola	0	0	3	insectivorous	forest	low	native

Myiozetetes similis	1	0	0	omnivorous	generalists	medium	native
Nystalus maculatus	1	0	0	insectivorous	generalists	medium	native
Paroaria dominicana	75	8	24	omnivorous	open	high	endemic
Passer domesticus	39	14	0	omnivorous	generalists	high	non-native
Patagioenas picazuro	0	0	12	granivorous	generalists	medium	native
Phaeomyias murina	0	2	15	omnivorous	open	high	native
Picumnus pygmaeus	0	0	2	insectivorous	forest	low	endemic
Pitangus sulphuratus	34	6	59	omnivorous	open	high	native
Polioptila plumbea	0	0	27	insectivorous	generalists	high	native
Pseudoseisura cristata	1	0	27	omnivorous	generalists	high	endemic
Rupornis magnirostris	0	1	8	carnivorous	open	high	native
Sittasomus griseicapillus	1	0	0	omnivorous	forest	low	native
Sporophila albogularis	102	37	15	granivorous	open	high	endemic
Sturnella superciliaris	0	0	3	omnivorous	open	high	native
Synallaxis hellmayri	0	0	9	insectivorous	open	high	endemic
Tachornis squamata	1	0	5	insectivorous	open	high	native
Thraupis sayaca	22	0	6	omnivorous	generalists	high	native
Todirostrum cinereum	1	0	5	insectivorous	generalists	high	native
Troglodytes aedon	2	0	4	insectivorous	open	high	native
Turdus amaurochalinus	4	4	6	omnivorous	generalists	high	native
Turdus leucomelas	0	0	4	omnivorous	generalists	high	native
Turdus rufiventris	41	11	10	omnivorous	open	high	native
Tyrannus melancholicus	19	4	27	omnivorous	open	high	native
Vanellus chilensis	32	2	16	insectivorous	open	high	native
Vireo chivi	0	0	5	insectivorous	forest	low	native
Volatinia jacarina	73	16	62	omnivorous	open	high	native
Zenaida auriculata	18	9	54	granivorous	open	high	native
Zonotrichia capensis	23	12	6	omnivorous	open	high	native

Chapter 3: Site selection methodology for UK vineyards project

© Natalia Zielonka: harvest in an English vineyard.

Natalia B. Zielonka

This chapter describes the site selection methodology I followed to choose sites for the research project across UK vineyards. These sites were used to collect data presented in ***Chapters 4-6****.*

3.1. Introduction

As reviewed in **Chapter 1** (General Introduction), the responses of biodiversity to landscape complexity, semi-natural habitat features, and on-farm management practices (general management regimes, such as organic farming, and finer scale diversification practices) are context-dependent, as are the resulting impacts on yields (Karp *et al.* 2018, Albrecht *et al.* 2020). To inform agricultural management, research should be performed at large-spatial scales to allow for the disentangling of landscape effects and to make results generalisable to wider industry, whilst also using robust (e.g. experimental methods with controls) methods that directly quantify biodiversity and its contributions to ecosystem services and disservices (Pejchar *et al.* 2018, Kleijn *et al.* 2019). Robust demonstrations of the effects of biodiversity for ecosystem service and disservice provision often originate from scattered case-studies (Kleijn *et al.* 2019), whilst landscape-scale studies often lack direct manipulation of conditions or measurements of services or yield (Gurr *et al.* 2016, Gillespie *et al.* 2017).

Understandably, it is logistically challenging and expensive to apply classical experimental methods involving treatments and controls, whilst ensuring random distribution of sampling points across large spatial scales (e.g. Rundlöf *et al.* 2015; reviewed by Gillespie *et al.* 2017). A solution to this in landscape ecology is to make use of *'natural experiments'*, which make use of already existing environmental gradients, brought on by natural patterns or human intervention (e.g. intensity of agricultural practices). To further improve the robustness of natural experiments for the purposes of making generalisable conclusions, which would ideally include the control of some variables, non-random selection of sites can be used, which gives rise to '*pseudo-experiments'* (Gillespie *et al.* 2017). Non-random approaches to site selection allow greater control over spatial independence of sites and collinearity between variables than may otherwise arise and have major impacts on the inferences made across landscape scales (Eigenbrod *et al.* 2011).

There are recent examples of non-random site selection in ecological research, though the application of this approach has been limited to only a couple of variables and a subjective selection of regions (as reviewed by Gillespie *et al.* 2017). To ensure generalisability of results, the consideration of multiple variables and across broader scales may be necessary. To address this issue, Gillespie *et al.* (2017) has set out an 'objective site selection protocol', which aims to choose sites that contrast as much as possible in key variables, whilst being representative of the broader system. Gillespie *et al.*'s approach was originally developed to study the links between land-use, management variables and insect pollinator communities within agricultural landscapes, making it highly relevant to our study. The three objectives of this approach are:

(i) Objective site selection, which has transparent methodology;
(ii) Consideration of multiple variables, and interactions between them, to enable selection of sites most contrasting along multiple gradients;
(iii) Enhancing generalisation of findings by choosing sites that are representative of the entire study system.

Ensuring sufficient power to detect existing effects ensures research effectiveness, and underpowered and overpowered studies may result in wasted resources or excessive resource use. Due to the logistical and financial challenges associated with ecological research, a lot of field studies have low statistical power (Lemoine *et al.* 2016). Power analyses can be used prior to data collection to inform sufficient level of sampling and help optimise study design. Power analyses determine the probability that an observed effect will be statistically detected, given the sample size and the expected magnitude of the effect, which can be informed by published literature or a pilot study (Green & MacLeod 2016). Power analyses aim to predict the power of a study design, and to estimate the sample size required to achieve 80% confidence of rejecting the null hypothesis when there is a true effect, avoiding a Type 2 error that could result from inadequate sampling intensity (Johnson *et al.* 2015; Green and MacLeod 2016).

Taken together, our site selection protocol was heavily based on Gillespie *et al.*'s (2017) approach, and included four stages:

(i) Stage 1: Power analysis to inform optimal sampling effort;
(ii) Stage 2: Compiling a list of candidate sites (UK vineyards);
(iii) Stage 3: Characterising candidate sites by key environmental and management variables;
(iv) Stage 4: Site selection following an algorithm.

3.2. Stage 1: Power analysis

We used the *simR* package in R (Green and MacLeod 2016), which performs power analyses for mixed models, using Monte Carlo simulations (999 permutations) to predict power. Our first objective (for **Chapter 4**) was to analyse the relative effects of landscape complexity, semi-natural habitat features and vineyard management on bird and arthropod biodiversity, as measured by abundance and diversity. Our second objective (for **Chapter 5**) was to quantify grape damage (through visual surveys and experimental exclusion) by bird and insect pests and relate the damage rates to landscape complexity, semi-natural habitat features and vineyard management predictors. We used published literature to inform the effect sizes of relevant predictors in the power analyses. The studies used to inform the power analysis for objective (1) are summarised in Table 3.1, and those used for objective (2) are summarised in Table 3.2. Whilst our aim was to also measure insect grape damage, the majority of studies that we used to inform the power analyses originated from birds, which were the primary focus of our research, and also a key grape pest in UK vineyards (Griffiths-Lee *et al.* 2022 and pers. obs.). We used these studies to make conservative assumptions that we tested through power analyses for our two objectives:

(1) Biodiversity power analysis:
    (i) Effect of semi-natural habitats is mostly positive and varies in studies between -0.2 – 0.8. We simulated effects of 0.1, 0.2 and 0.5.*
    (ii) The effect of organic in relation to conventional management is mostly positive but variable across studies: -0.67 – 2.7. We simulated the effects of 0.1, 0.25 and 0.4. *
(2) Bird grape damage power analysis
    (i) The effect size of bird exclusion on crop damage or on the abundances of invertebrate pests varied between -0.05 – 1.4, with most estimates being at the lower end. We simulated the effects of 0.1, 0.2 and 0.5.*
    (ii) The strength of the effect of distance to semi-natural habitats on ecosystem service and disservice provision varied between -0.01 – 0.6, and we simulated the effects of 0.05, 0.1 and 0.4.
    (iii) Only one study reported the effect of semi-natural habitat cover at the landscape scale and we simulated the effects of 0.3 and 0.5.

For both power analyses, we set the effect of year (assuming two sampling years) to be 0.2, and we set the random variation between sites to be 0.3. Note that we did not consider negative effect sizes as only the strength of the effect was important for the purposes of the power analyses. For each analysis, we allowed the simulated number of sites to vary between 0 and 25 and assumed 1-2 sampling locations (point counts for birds, and transects with pitfall traps for arthropods or exclusion treatments) per site.

Power analysis simulations indicated that 15 vineyards with at least 1-2 sampling locations per site would be necessary to achieve an 80% chance of detecting the effects of landscape complexity, semi-natural habitat features and farm management on biodiversity (Figure 3.1a). For the grape damage simulations, we found that 16 sites with 2 sampling points each (transects) would be necessary to detect the effects of bird and bird + insect exclusion on grape damage and yield (Figure 3.1b).

As we planned to gather finer-scale management predictors (e.g. agrochemical use, ground cover management practices), we aimed to select 18-20 study sites to ensure sufficient statistical power of detecting existing effects of predictors.

Table 3.1. Effect sizes in previously published literature of landscape composition, semi-natural habitats and farm management on biodiversity across different crop systems.

Crop	Tested effect	Taxa and response	Detected effect size	Reference
Strawberry	Semi-natural cover	Bird diversity	+ 0.4 – 0.5	(Gonthier *et al.* 2019)
	Semi-natural cover	Bird abundance	+ 0 – 0.8	
Apple	Wooded cover	Bird abundance	+ 0.5	(García *et al.* 2018)
	Wooded cover	Bird richness	+ 0.3	
Alfafa	Presence of edge habitats	Bird richness	+2.8	(Kross *et al.* 2016)
	Presence of edge habitats	Bird abundance	+3.9	
Winter cereals and spring oats	Organic management	Arthropod diversity	-0.2	(Shah *et al.* 2003)
	Organic management	Arthropod diversity	+ 0.05 – 2.7	
Grapes	Organic management	Bird and arthropod diversity	+ 0.25 – 0.5	(Puig-Montserrat *et al.* 2017)
	Woodland cover	Bird and arthropod diversity	+ 0.15 – 0.3	
Grapes	Organic management	Arthropod biodiversity	+ 0.23	(Bruggisser *et al.* 2010)
	Organic management	Arthropod biodiversity	+ 0.19	
Grapes	Organic management	Arthropod abundance	-0.1 - + 0.6	(Ostandie *et al.* 2021)
	Insecticide use	Arthropod abundance	-0.23	
	Semi-natural cover	Arthropod abundance	- 0.2 - + 0.4	
Grapes	Organic management	Arthropod abundance	-0.67	(Caprio & Rolando 2017)

Table 3.2. Effect sizes in published literature of birds and insects, and the relative effects of landscape composition, semi-natural habitats and farm management on the rates of crop damage.

Crop	Tested effect	Detected effect size	Reference
Cacao	Bird exclusion on insect herbivore abundance	+ 0.2 – 0.5	(Maas *et al.* 2013)
	Bird exclusion on yield	-0.5	
Strawberry	Bird exclusion on natural control	-0.04	(Gonthier *et al.* 2019)
	Bird exclusion on crop damage	+ 0.04	
Strawberry	Bird exclusion on crop damage	-0.04	(Olimpi *et al.* 2020)
	Bird exclusion on pest abundance	+0.05	
Apple	Bird exclusion on insect damage	+ 0.13	(Peisley *et al.* 2016)
Apple	Bird exclusion on pest damage	+ 1.5	(García *et al.* 2018)
	Bird exclusion on natural enemy abundance	+ 0.6	
Coffee	Bird exclusion on insect herbivore abundance	+0.5	(Johnson *et al.* 2010)
	Bird exclusion on herbivory	+ 0.3	
Apple	Bird exclusion on biomass of arthropod pests	+1.4	(Martínez-Sastre *et al.* 2020)
	Bird richness on biological pest control	+0.33	
Apple	Bird exclusion on yield	+ 0.1	(Saunders & Luck 2016)
	Bird exclusion on fruit set	-0.05	
Cabbage	Bird exclusion on herbivory	-0.4	(Martin *et al.* 2013)
Grapes	Distance from edge on crop damage by birds	-0.01	(Peisley *et al.* 2017)
Strawberry	Distance to non-crop edge on arthropod natural enemy presence	-0.02 - + 0.6	(Olimpi *et al.* 2020)
	Proportion semi-natural cover on arthropod natural enemy presence	+ 0.7	

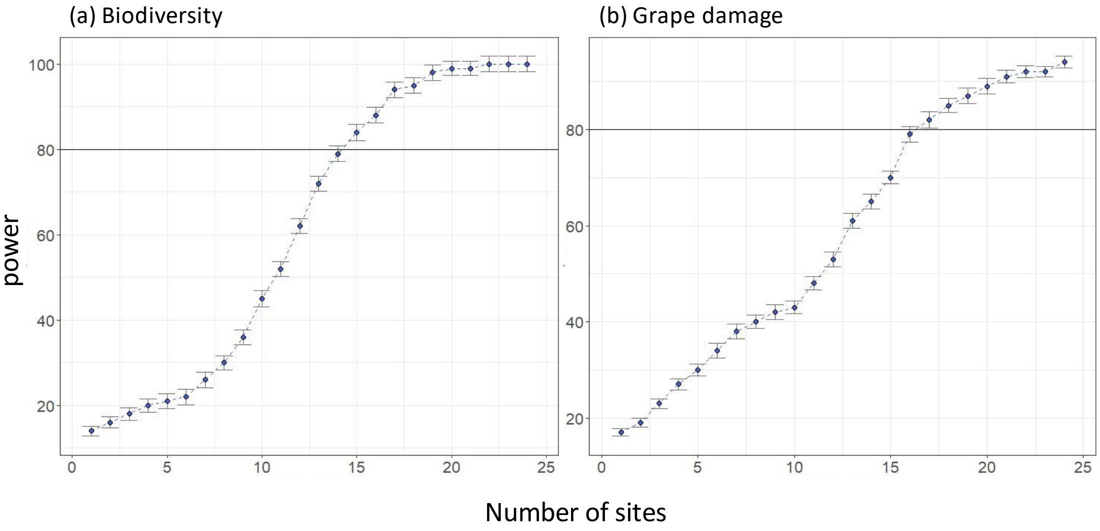

Figure 3.1. Percent power (±95% CI) to detect the effects of landscape complexity, semi-natural habitat features and vineyard management ('organic' vs 'non-organic') on biodiversity (**a**), and the effect of bird and insect exclusion (bird-only, bird + insect, control) on grape damage (**b**). Power analyses assumed one bird point count location, and *two transects* for arthropod sampling, exclusion experiments and grape damage assessments per site. Simulated effect size estimates for vineyard management, landscape complexity and distance to the edge were informed by published literature (Tables 3.1 and 3.2). The effect of sampling year (one of two) was set to be 0.*2*, and the random effect of site was set to 0.3 Power analyses were performed using the package simR in R (Green and Macleod 2016).

3.3. Stage 2: Compiling a list of candidate sites (UK vineyards)

Following the power analyses, we proceeded with stages 2-4 of the objective site selection protocol, which are summarised in Figure 3.2.

To compile a list of candidate sites, we held a webinar in November 2020 with members of WineGB (association of wine growers and makers in Great Britain) to share our project proposal and to refine research priorities in communication with wine grape growers. Following the webinar, we sent out an expression of interest form (Supplementary material S3.1) using the WineGB mailing lists, which targeted UK vineyard managers. The form collected basic details about each vineyard that would be used in selecting vineyards at stage 3, including vineyard age and size, approximate location, management style (e.g. certified organic, conventional) and grape varieties grown. This yielded a list of 80 interested vineyards, which *became 'candidate study sites'* and moved to stage 3 (Figure 3.2).

3.4. Stage 3: Characterising candidate sites by key environmental and management variables

We used UK vineyard hectarage data (Skelton, 2022) to identify the key winegrowing regions of the UK (Figure 3.3). This showed that the industry is concentrated in southern England and by hectarage, the key regions are: Kent (1012 ha), West Sussex (457 ha), East Sussex (382 ha) and Hampshire (340 ha). This encompasses the South Downs National Park, where there has been a 90% increase in the hectarage since 2016, with a further 40,000 ha of the National Park area being considered suitable for viticulture under current predictions of temperature increases (South Downs National Park Authority 2021). To ensure we captured the key winegrowing regions of the UK and to increase the generalisability of our results, we defined the following as focal regions: southeast England (Kent, East Sussex and East Anglia), central south England (Essex, Surrey, West Sussex and Hampshire), and southwest England (Dorset, Gloucestershire, Wiltshire and Herefordshire, Figure 3.3).

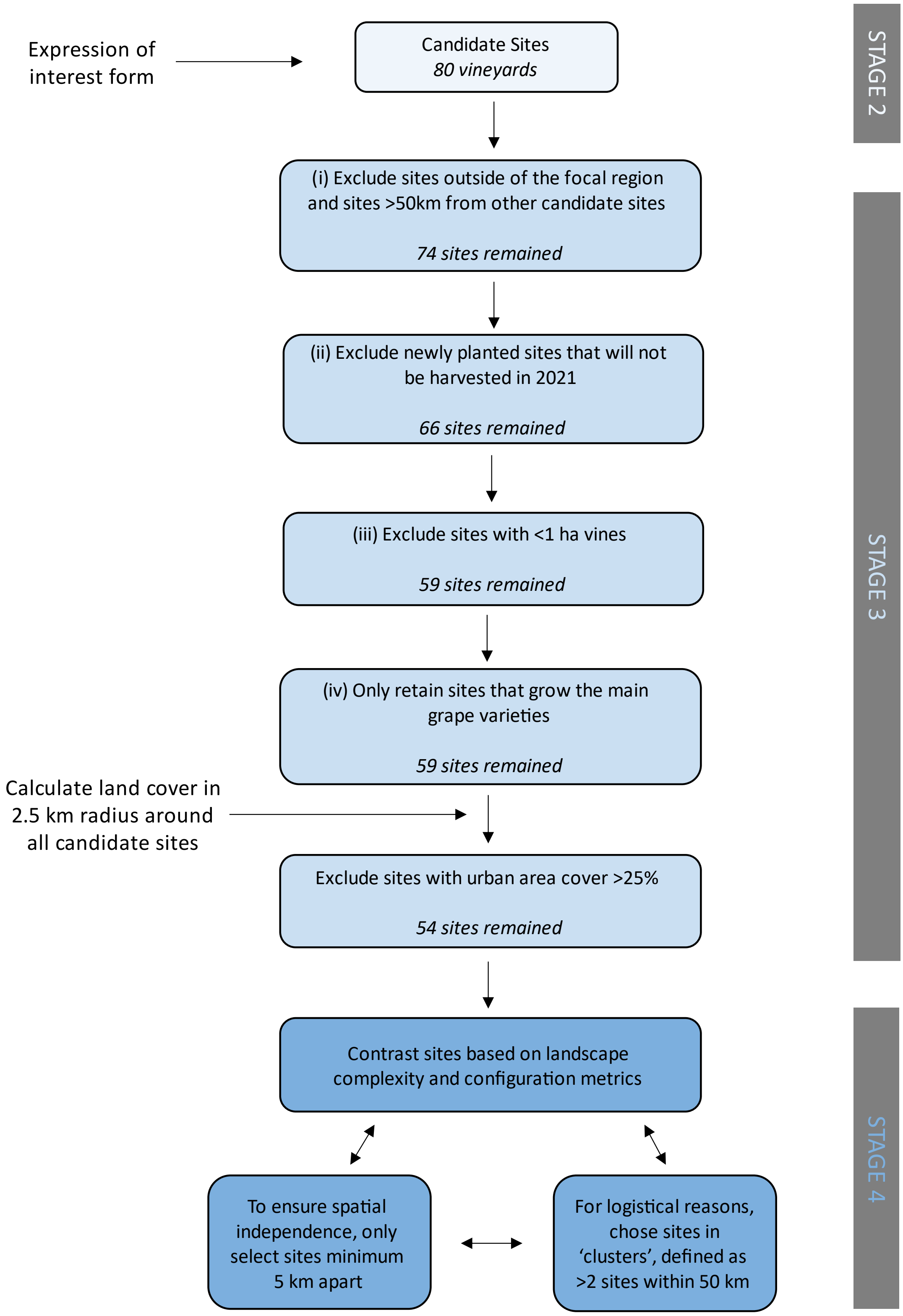

Figure 3.2. A schematic of the three-stage site selection protocol that was followed to select study sites. The protocol was informed by the 'objective site selection' framework set out by Gillespie *et al.* 2017 (see section 3.1.).

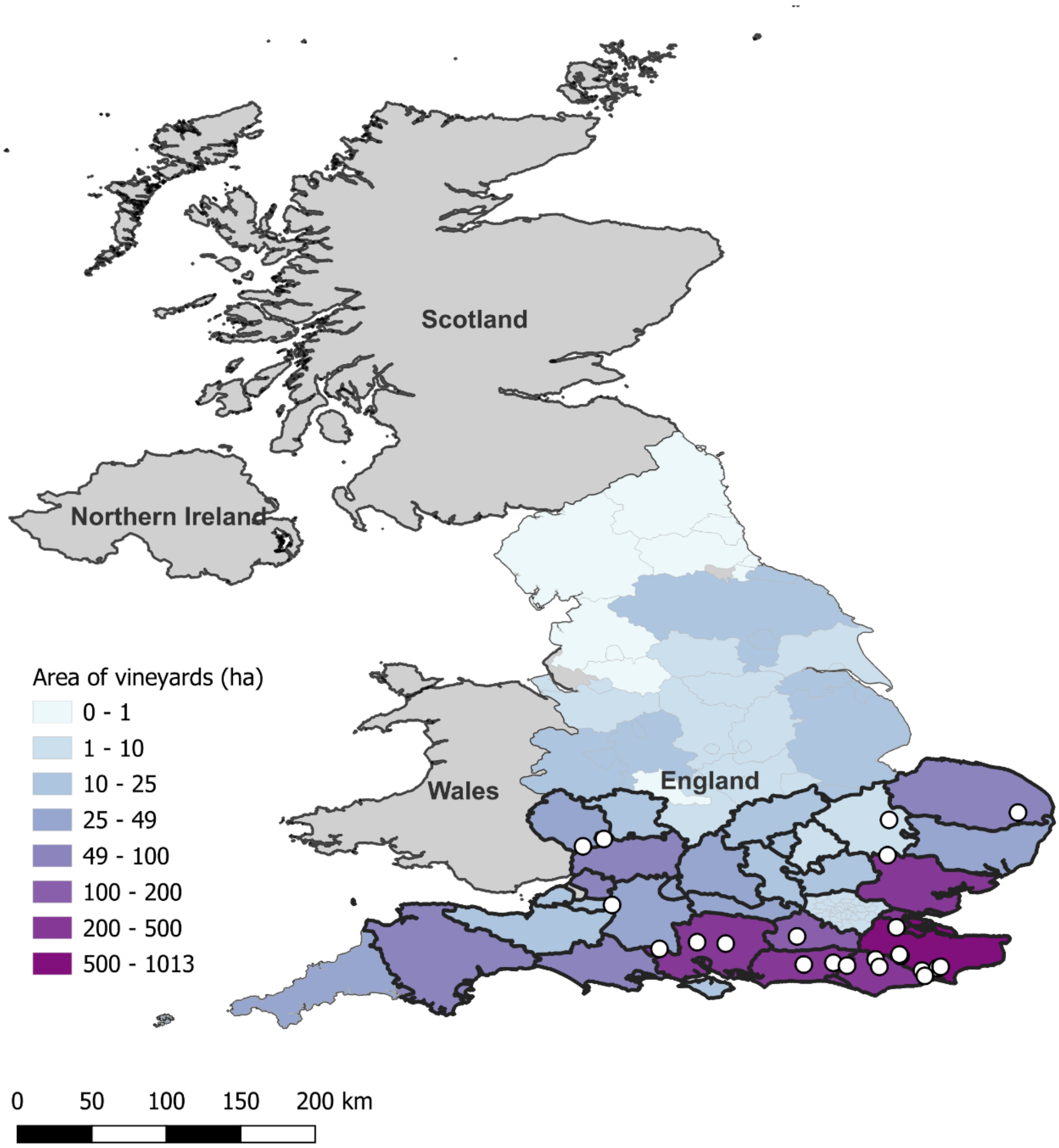

Figure 3.3. A map of the UK showing the area, in hectares, of commercial vineyards per county in England. Counties in bold, black outline indicate the 'focal area' (see *section* 3.4.). The white circles indicate the final selected study sites [n=22; note that there are 21 circles as two of the sites were in the same location with different management (organic or non-organic) being applied to different fields – see *section* 3.5 for details). Hectarage data were from EnglishWine.com, compiled by Stephen Skelton, and accurate in March 2022.

Using information from the expression of interest form, we excluded candidate sites that did not meet one, or more, of following criteria:

(i) Sites have to be within focal study region (Figure 3.3).

(ii) Sites have to be within <50 km from other candidate sites.

(iii) Sites need to yield grapes in the study years (2021 and 2022). First grape harvests are expected three years after planting, so we excluded vineyards planted after 2018.

(iv) Sites need to be at least 1 ha in size to ensure they are sufficiently large to have two sampling points for arthropod surveys (at least 30 m apart), and for bird point count locations to be within vine fields, at least 50 m away from field edges.

(v) Sites need to grow at least one of the key UK grape varieties: Chardonnay, Pinor Noir, Piot Meunier, and Bacchus (WineGB 2022). This was important to control as varieties vary in harvest times, and grape damage by birds can differ between varieties (Nereu *et al.* 2018)

For each of the remaining sites, we quantified five landscape composition and complexity metrics that have been shown to affect on-farm biodiversity (see Chapter 1 and Tables 3.1 and 3.2):

(i) *Percent semi-natural cover*: summed cover of deciduous woodland, coniferous woodland, semi-natural grasslands (neutral, calcareous, acid grassland and fenland), heathland, heather grassland and bog.

(ii) *Percent arable and pasture cover*: summed cover of arable and improved grassland.

(iii) *Percent urban cover*: summed cover of urban and suburban areas.

(iv) *Simpson's index of diversity*: this measure of habitat diversity quantifies the probability that two random cells belong to the same habitat class. Simple, homogenous landscapes have higher values, and heterogenous, diverse landscapes have lower values.

(v) *Total edge length:* total length of edges between two habitat classes (e.g. woodland and arable), a measure of landscape configuration.

We used the UK Centre for Ecology & Hydrology land cover map 2019 (Marston *et al.* 2022) to characterise the landscape composition and configuration within 2.5 km radius buffer around the central point of each candidate study sites. A polygon map at the resolution of 25 m (vector) was used and all variable calculations took place in ArcGIS 10.6.1 (ESRI 2018) and FRAGSTATS 4.2 (McGarigal *et al.* 2002). We calculated Pearson's correlation coefficients to test for collinearity between the metrics (Dormann *et al.* 2013), and found percent semi-natural cover (i) and percent arable and pasture cover (ii) to be negatively correlated ($r(58) = -0.661$, $p\text{-value} < 0.05$), so only percent semi-natural cover was used in stage 4 of the site selection.

3.5. Stage 4: Site selection following an algorithm.

We standardised the landscape composition and complexity metrics using a Box-Cox transformation, which converted raw values to z-scores for each site. Z-score measures the number of standard deviations from the mean, calculated following this equation:

$$Z = (x-\mu)/\sigma$$

x = variable value for a given site

μ = mean of all values of x across sites

σ = standard deviation of all the values of x across sites

We calculated the z-scores for the two vineyard management styles (organic and non-organic) separately, which gave us different values of μ and σ for the two groups. The means of the four landscape metrics were not significantly different between the two management groups (*semi-natural cover*: $t(58) = 0.839$, p-value = 0.414; *Simpson's index*: $t(58) = 1.619$, p-value = 0.114; *urban cover*: $t(58) = 1.121$, p-value = 0.314; *edge length:* $t(58) = 1.490$, p-value = 0.143).

Five candidate study sites were characterised by a high urban and sub-urban cover (> 25%), which may have had a strong effect on the observed biodiversity. These sites did not contrast in the other metrics, preventing us from testing the relative effects of landscape and management metrics so they were excluded from the site selection (Figure 3.2). The percent cover by urban features across the remaining candidate sites varied between 0.2-16.9%, and this left three metrics for consideration.

Before making the final selection, we imposed two further criteria:

(i) Selected sites would need to be at least 5 km (linear distance) away from other selected sites to ensure spatial independence of sites at the landscape scale.

(ii) For logistical reasons, we set the maximum distance between vineyards within a cluster to 50 km. We defined 'a cluster' as an area of 2+ study sites (>5 km, <50 km) and these were largely linked to different regions of England (e.g. southeast included Kent and East Sussex sites).

The remaining candidate sites varied in three landscape metrics. In the landscape buffer, percent cover by semi-natural habitat varied between 3.6-60.1% (z-scores -2.41 – 6.03, respectively); Simpson's index of diversity varied between 0.25 (heterogenous) – 1.47 (homogenous; z-score -1.80 – 6.69); and total length of edges varied between 76,225 – 224,175 m (z-score -3.72 – 2.00).

Study sites were selected by inspecting the z-scores for the three remaining metrics and choosing candidate sites with the highest and lowest Z-scores (Figure 3.4). Within each management type, sites with the highest and lowest z-scores were matched by size; for example, two non-organic sites with z-score of – 1.4 and + 1.4 for percent semi-natural cover, which corresponded to ~10% and ~29% semi-natural cover within the 2,500 m radius, respectively, were matched as they were 30 and 26 ha in size. When considering the z-scores for the three metrics, percent semi-natural cover was inspected first, given how widely it has been evidenced to impact biodiversity and ecosystem functions, followed by the total edge length and the Simpson's index.

We followed this protocol to select 20 vineyards (8 that described themselves as 'organic', and 12 that were 'non-organic'). Two of the selected sites did not meet the spatial independence condition as they were not 5 km apart because two separately managed vineyards were present and intertwined across one 'site' with half the fields being managed organically and the other half non-organically. These vineyards were good candidate sites upon z-score inspection, and as the choice of organic vineyards was limited, we decided to proceed with working with both vineyards, and treating them as independent data points. Whilst we were aware that spatial autocorrelation could be an issue across these sites, we considered it also a good, though anecdotal, opportunity to single-out the effects of management on biodiversity.

Following data collection in 2021, early results indicated differences in bird diversity between organic and non-organic sites, though the effect sizes were small. To ensure sufficient sampling to maximise the likelihood of detecting a real effect, if there was one, we increased our sampling efforts at organic vineyards by recruiting two further sites. These two sites were recruited spontaneously and were not in our original sample of candidate sites. One site met all the conditions specified above, whilst the landscape buffer of the other site partially overlapped with the buffer of an existing site (distance between sites was 4.5 km). All 22 study sites are shown in Figure 3.3.

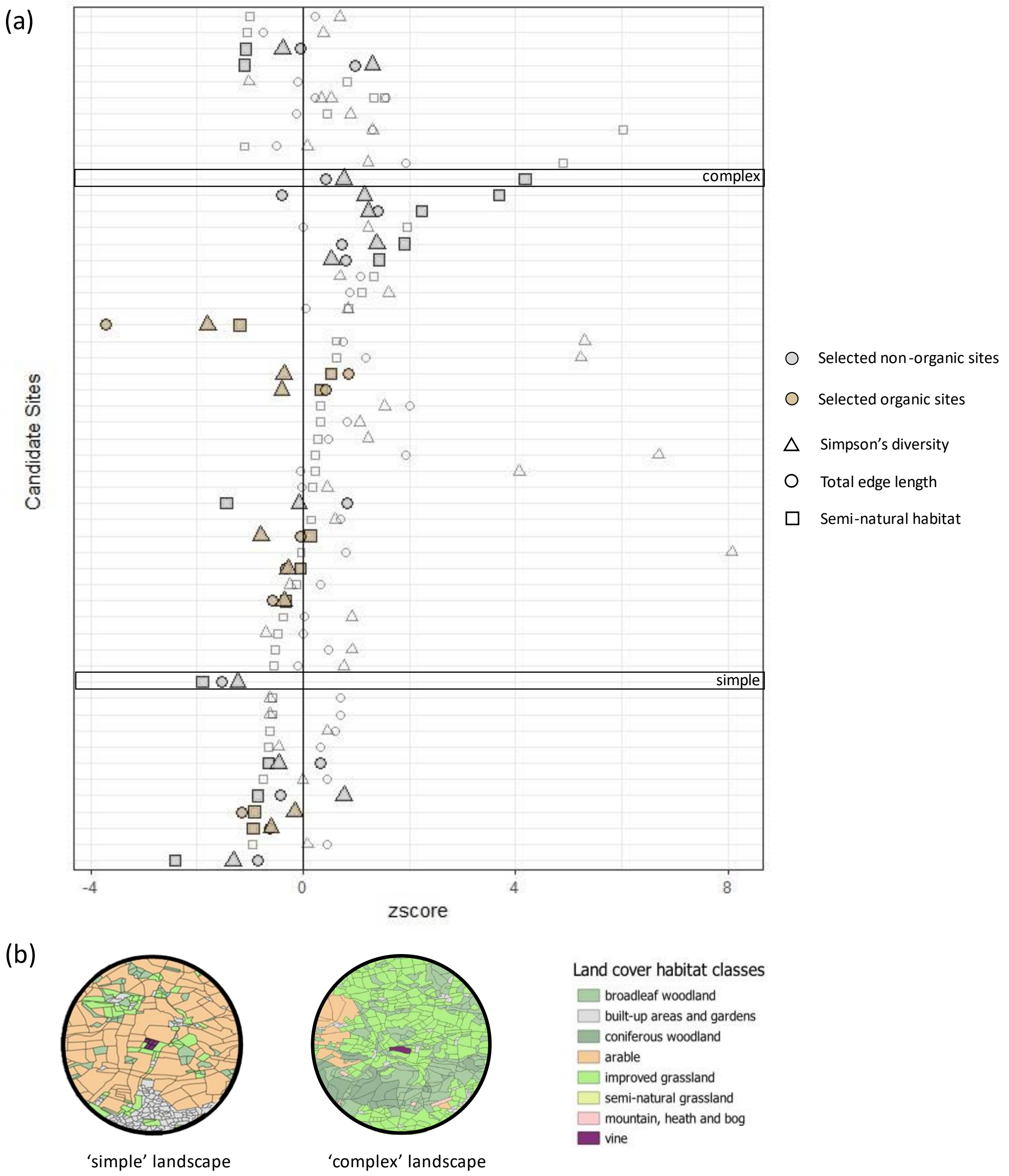

Figure 3.4. Z-scores **(a)** of three landscape complexity and configuration variables, calculated within 2.5 km buffer of the candidate sites (n=54). The variables were (see 3.4 for details): the Simpson's index of landscape diversity (triangle), proportion cover by semi-natural habitats (square), and the total edge length (circle). Unfilled shapes indicate z-scores for unselected candidate sites, and filled shape indicate selected sites (beige = organic, n=8; grey = non-organic, n=12). Two landscape habitat cover maps of selected vineyards are shown in **(b),** with an example vineyard in a 'simple' landscape, characterised by negative z-scores, compared to a 'complex' landscape that is characterised by positive z-scores.

3.6. Description of study sites

The project took place across 22 English vineyards, with average vine hectarage of 24.39 ha (ranging between 1 – 182 ha). Ten of the sites were certified organic, and the remaining 12 were classed as non-organic, of which, in the expression of interest form (section 3.3), four identified themselves as 'minimal input', or 'sustainable', and the remaining 8 as 'conventional'. Though we did not consider accreditation through the Sustainable Wines of Great Britain (SWGB, Chapter 1) scheme in our study selection process, as the scheme was only launched in 2020 (SWGB 2020) with the first set of vineyards becoming accredited in 2021, by the time of data collection, 11 of our study sites were SWGB-accredited, and three sites were accredited through both schemes. Summary vineyard and landscape complexity and configuration variables for study sites accredited through one of the two schemes are given in Table 3.3.

Table 3.3. Summary descriptive statistics (mean ± SE) comparing vineyard and landscape complexity and configuration variables between certified-organic (n=10) and non-organic sites (n=12), and between SWGB-accredited (n=11) and non-SWGB (n=11) sites. Composition and configuration of semi-natural habitats around study sites was measured within 2.5 km radius buffers around each site (n=22).

	Certified-organic	Non-organic	SWGB-accredited	Non-SWGB
Proportion woodland cover	0.171 ± 0.026	0.168 ± 0.035	0.160 ± 0.010	0.179 ± 0.010
Proportion semi-natural habitats	0.025 ± 0.013	0.010 ± 0.004	0.017 ± 0.011	0.016 ± 0.003
Landscape edge density	119.02 ± 7.64	118.23 ± 8.85	124.05 ± 2.39	112.35 ± 2.52
Vineyard size (ha)	33.9 ± 19.7	17.3 ± 6.62	35.19 ± 4.90	12.50 ± 1.91
Field size (ha)	2.31 ± 0.091	2.70 ± 0.054	2.94 ± 0.23	1.99 ± 0.374
Field edge density (m/ha)	368.0 ± 8.13	279.0 ± 13.8	347.0 ± 12.5	295.1 ± 11.4

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Chapter 3 Supplementary Materials

S3.1 - Expression of interest form for site selection

Q1 Please provide your farm name:

Q2 What is your vineyard production areas (acres)?

Q3 What is your vineyard management style? (please tick all that apply)

Conventional, Organic, Biodynamic, Other (please specify)

Q4 What varieties of grapes do you grow? [text box]

Q5 How would you describe your vineyard?

Monoculture – grapes are the only crop grown within the property, Monoculture but other crops are grown within the property, Crop-livestock system, Polyculture, Other (please specify)

Q6 If you have any additional comments, please feel free to write them here:

Chapter 4: Management practices, and not surrounding habitats, drive bird and arthropod biodiversity within vineyards.

© Natalia Zielonka: ladybird (family: Coccinellidae) on a vine plant in an English vineyard.

Natalia B. Zielonka[a], Jack D. Shutt[b], Simon J. Butler[a*] & Lynn V. Dicks[a,b*]

[a] School of Biological Sciences, University of East Anglia, Norwich, UK, NR4 7TJ
[b] Department of Zoology, University of Cambridge, UK, CB2 3EJ

* *joint last authors*

Abstract

Agrochemical use and habitat loss associated with agriculture are drivers of biodiversity loss worldwide, and biodiversity-friendly farming practices, including organic management, are increasingly promoted by policy and industry in an attempt to offset this. Grapes are an important perennial crop globally, and in the UK, viticulture is the fastest growing agricultural sector and sustainable vineyard management is promoted by the Sustainable Wines of Great Britain 'SWGB' scheme. Here, we performed the first assessment of the simultaneous effects of surrounding habitats and vineyard management practices on bird and arthropod biodiversity across 22 English vineyards (10 certified-organic, 11 SWGB-accredited, and 3 both). We surveyed birds using point counts and arthropods with pitfall traps, and used linear mixed modelling to relate diversity and abundance to habitat and management predictors at landscape and local scales. We show that arthropod abundance is significantly higher on organic vineyards, whilst bird diversity is significantly lower on SWGB-accredited vineyards, but we find no other significant effects of organic certification or SWGB-accreditation on biodiversity. We also find no significant effects of the surrounding habitat structure on the biodiversity of birds and arthropods. Instead, we show that ecotoxicity scores derived from agrochemical use data have a significant negative impact on bird diversity, and on arthropod abundance and diversity. Organic status predicts a significant reduction in ecotoxicity scores, but only when application frequency is not considered, and contradictorily, SWGB-accredited vineyards have higher ecotoxicity scores than those without accreditation. Ground vegetation cover has a consistent, positive effect on bird and arthropod diversity, with model predicted diversity increasing 1.5 and 2.5-fold, respectively, in vineyards with the highest vegetation cover, and herbicide use has a negative effect on the vegetation cover. Our research demonstrates that individual management practices have a stronger effect on vineyard biodiversity than the habitat context, overall management regime or certification. Our study sets an important baseline for vineyard management and accreditation schemes and generates key recommendations for improvement. To benefit biodiversity within vineyards, we

recommend that sustainability accreditation schemes include requirements to reduce the ecotoxicity of used agrochemicals, and promote higher ground vegetation cover and height by reducing herbicide use.

Highlights

- Organic vineyards support higher arthropod abundance but have no effect on birds.
- Vineyards accredited through a sustainability scheme host lower bird diversity.
- Landscape structure does not affect vineyard biodiversity.
- Ecotoxicity scores based on agrochemical use have detrimental effects on biodiversity.
- Higher ground vegetation cover supports biodiversity in vineyards.

Acknowledgements

We sincerely thank our study vineyards' managers and employees for access to field sites, in-field logistics, for providing management information, and their support and interest in our research. We thank WineGB and SWGB, and Chris Foss in particular, for their help in setting up this project and for supporting our research. We thank Madeleine Judge, Amy Hollingworth, Liam Smith and Katarzyna Zielonka for their assistance in fieldwork. This work and Natalia Zielonka were funded by the UKRI Biotechnology and Biological Sciences Research Council Norwich Research Park Biosciences Doctoral Training Partnership [Grant number BB/M011216/1].

4.1. Introduction

Habitat loss, landscape simplification and increased chemical use associated with agricultural expansion and intensification are major causes of biodiversity loss globally (Newbold *et al.*, 2016; Pereira *et al.*, 2012). A recent Europe-wide analysis found agricultural intensification, and particularly the associated agrochemical use, to be the main driver of most bird population declines (Rigal *et al.*, 2023). Similarly, a global study found terrestrial arthropod abundance and biomass to have been steadily declining by ~9% per decade, supporting strong declines in Europe and a negative relationship with land use change (van Klink *et al.*, 2020). These declines not only risk extinctions of rare species, but also threaten the loss of key ecosystem functions that benefit agriculture (Hendershot *et al.*, 2020).

Grapevines are an important global crop, with over 7 million hectares of land dedicated to their production, which accounts for about 5% of the global cover by perennial crops (Ritchie & Roser, 2013; Venkitasamy *et al.*, 2019). At landscape scale, increased vineyard cover has been shown to have a detrimental effect on biodiversity, including on birds (Assandri *et al.*, 2016; Pithon *et al.*, 2016), bats (Rodríguez-San Pedro *et al.*, 2019), and arthropods (Geldenhuys *et al.*, 2022). However, maintaining habitat heterogeneity, through habitat retention and provision within vineyards can help offset these impacts (Paiola *et al.*, 2020; Winter *et al.*, 2018), particularly in more homogenous landscapes where resources are otherwise limited (Assandri *et al.*, 2016; Martin *et al.*, 2019). For example, retention of native woodlands and hedgerows within Swiss (Guyot *et al.*, 2017), German (Rösch *et al.*, 2023), and Chilean vineyards (Muñoz-Sáez *et al.*, 2020; Steel *et al.*, 2017) enhanced bird abundance and diversity, whilst wildflower mixes and reduced mowing that increased ground vegetation cover benefited arthropod and bird diversity in European (Griffiths-Lee *et al.*, 2023; Puig-Montserrat *et al.*, 2017) and South African vineyards (Geldenhuys *et al.*, 2022). Studies from Europe (Brambilla *et al.*, 2017), and South America

(Muñoz-Sáez *et al.*, 2020) have also demonstrated the potential for vineyards to support high abundances of threatened and endemic bird species.

The viticultural industry faces pressure to move towards more environmentally sustainable management (Barbaro *et al.*, 2021; Merot *et al.*, 2019), intensified by the new Global Biodiversity Framework, which sets a target to manage agricultural landscapes sustainably, '*including through a substantial increase of the application of biodiversity friendly practices*' (Keping, 2023). Managing agricultural landscapes in ways that are less detrimental to biodiversity is often encouraged through agri-environmental schemes and accreditations, and rewarded through compensation or higher product prices (Boetzl *et al.*, 2021; Tscharntke *et al.*, 2012). Globally, organic farming has been shown to enhance species richness on agricultural land by an average of 30%, though this positive effect is greater in more homogenous and intensively-managed agricultural landscapes (Tuck *et al.*, 2014). Across vineyards, a weak positive effect of organic viticulture on biodiversity has been observed (Paiola *et al.*, 2020; Rollan *et al.*, 2019), though this varied across taxa, and was generally stronger for highly mobile taxa, such as birds, than for plants or ground-dwelling arthropods (Assandri *et al.*, 2016; Froidevaux *et al.*, 2017; Fuller *et al.*, 2005; Ostandie *et al.*, 2021; Puig-Montserrat *et al.*, 2017). The effects of organic viticulture have not been consistent across studies (Paiola *et al.*, 2020) and complementary habitat provision within vineyards seems essential to achieving benefits for biodiversity (Barbaro *et al.*, 2021).

In the UK, the viticultural industry is the fastest growing agricultural sector, attributed to increasing summer temperatures making the climate increasingly comparable to other European wine-growing regions (Nesbitt *et al.*, 2019). Due to the recent expansion, specific recommendations for UK viticulture are lacking, and research is limited, though a recent industry survey found heavy reliance on agrochemicals (Griffiths-Lee *et al.*, 2022). To address this, a national sustainability scheme called Sustainable Wines of Great Britain (henceforth 'SWGB') was launched in 2020 and it so far accredits ~55% of the UK's vineyard hectarage (WineGB, 2022).

However, the scheme lacks minimal requirements or specific targets, and rather members commit to a continual cycle of improvement towards sustainability, with minimal agrochemical use and biodiversity conservation strongly encouraged.

By working in multiple English vineyards spanning a range of management practices, and also varying in the structure of their surrounding landscapes, we provide the first simultaneous assessment of the effects of surrounding semi-natural habitats and management on vineyard biodiversity. Our aims were: (1) to assess the relative impact of surrounding habitat structure and vineyard management on bird and arthropod abundance and diversity, and (2) to compare bird and arthropod abundance and diversity between certified-organic and non-organic vineyards, and based on SWGB accreditation status. Due to their differing mobility, we predict surrounding semi-natural habitats to have a stronger effect on birds than on arthropods, while in contrast we predict arthropods to be more strongly affected by vineyard management, including organic viticulture, which we expect to have an overall positive effect on biodiversity.

4.2. Methods

4.2.1. Study vineyards

This study took place within 22 English vineyards from across the UK's key wine-growing regions (Figure S3.1). Sites were chosen to represent the broader English vineyard industry, with 10 sites being certified organic, and 11 being accredited through the SWGB scheme (three sites were accredited through both). Sites were selected using an objective site selection protocol following Gillespie *et al.*, (2017) to maximise landscape structure and management gradients. Full details are given in Chapter 3, and the gradients are described in 4.3.

4.2.2. Biodiversity sampling

We sampled bird and arthropod communities in 2021 and 2022, repeating surveys three times each year, with sampling seasons aligning with the key stages of the vine lifecycle ('budding': early to mid-April; 'flowering': late June-mid-July; 'harvest': mid-September to mid-October). See diagram of biodiversity sampling in Supplementary materials S4.1.

Birds

We performed 10-minute point counts across 44 locations during each survey season (average 1.81 ± 0.18 SE point counts per site, range 1-4, depending on vineyard size), and in total, we performed 222-point counts across the six sampling periods. We aimed to conduct a survey at all 44 locations each sampling period, but this was limited by poor weather and access restrictions, thus we performed between 35-40 point counts per period. Point count locations were placed in vine fields, at least 50 m from boundary habitats, and minimum 250 m from other point count locations. During the surveys, all birds seen and heard within a 50 m radius were recorded, excluding birds flying over. All surveys were conducted between 05:00 – 09:00 and within 3 hours of sunrise, which varied between sampling seasons. Surveys only took place on dry and still days (Bibby *et al.*, 2000), and were performed by the same observer.

Arthropods

Arthropod communities were sampled using pitfall traps along 79 transects across 21 vineyards each survey season (average of 3.85 ± 1.89 SD transects, range 2-10). We deployed pitfall traps along transects running perpendicular to the field boundary, with traps placed directly underneath vines at 20-meter intervals. Transects varied in length depending on field size and were 40 (3 traps, n=10 transects), 60 (4 traps, n=37) or 80 (5 traps, n=30) metresin length. Transects ran from 3 distinct boundary types: woodland (n=32 transects), hedgerow (n=32), or open boundary lacking any features (n=15). We aimed to evenly distribute transects of different lengths and from different boundary types between certified-organic and non-organic, and between SWGB-accredited and non-SWGB vineyards. This was possible for hedge and woodland transects up to 60 m in length, but out of the 16 open-boundary transects, 15 were in non-organic and 14 in SWGB-accredited vineyards, whilst of the 38 80-meter transects, 33 were in non-organic and 31 in non-SWGB vineyards.

We used pitfall traps to sample arthropods methodology (following methodology from Brown & Matthews, 2016), deploying 1,713 traps across the six sampling periods (average 291 per sampling period, range: 237-316; totalling 786 in 2021, and 927 in 2022). Clear plastic cups with 10 cm diameter were placed in the ground with the cup lip flush with the soil surface, and covered with a metal mesh square (0.8 cm mesh size) to reduce by-catch. Traps were filled with ~50 ml of water with organic unscented washing up detergent (10 ml detergent per 5L water) and left for 24 hours after which the catch was drained, and any earthworms and slugs were discarded. Collected specimens were stored in 75% ethanol. Across the sampling seasons, 34 traps were damaged or destroyed, and catch from these was discarded. All arthropods were identified to order level.

4.2.3. Characterising landscape structure and vineyard management

Habitat characteristics

We mapped the landcover habitats using the CEH Land cover 2021 map (Marston *et al.*, 2022) at two spatial scales. First, we used a 'landscape-scale' buffer of 2.5 km around a central point of each site, which was large enough to encompass the whole of our largest site, whilst it minimised the overlap of buffers between sites. Except for two site pairs, the landscape buffers did not overlap and were spatially independent. Secondly, we used a 'local-scale' buffer of 200 m around bird point count locations, and 100 m around arthropod transects, which was informed by similar studies (Barbaro *et al.*, 2021; Caprio *et al.*, 2015). At both scales, we calculated the cover by woodland (combining coniferous and deciduous), semi-natural grassland and agricultural (including improved grassland) areas, as well as total vine area, the average field size, and edge density. The presence of freshwater bodies was limited (at most constituting 0.02% of the landscape buffer), so instead, we calculated the length of '*linear water features'*, which included rivers and streams, though this predictor was only calculated at the landscape-scale, as rivers and streams were absent from the local scale. At the local scale, we calculated the length of '*linear wooded features'* which included hedgerows and tree lines within vineyards. We performed this in QGIS (3.30.00).

The amount of semi-natural habitats around our study sites ranged between <1% and 42% in a 2.5 km radius buffer (Figure 4.1) and the vineyards also varied in vine hectarage, which ranged between 1-182 ha (mean 24.39 ha). However, neither the surrounding habitats nor vineyard size varied significantly between organic and non-organic, nor between SWGB-accredited and non-SWGB sites (Chapter 3). Mean field size was significantly larger at SWGB-accredited (4.50 ha ± 0.02) than non-SWGB sites (4.16 ± 0.04, $t(19) = 2.617$, $p = 0.017$).

Management

Ground vegetation cover across English vineyards varies across the vine lifecycle and between sites (Supplementary materials S4.2), and to measure this variation, at 0 and 40 m along one arthropod transect in each sampling field, we measured sward height across the alleyway between two vine rows (18-22 measurements per alleyway, depending on its width), and we also estimated proportion of bare ground, to the nearest 5%, using a randomly placed 50x50 cm quadrat. We computed a crude *ground vegetation cover* metric from these measurements: *veg cover = µ [ground vegetation height] * (1 – proportion bare ground),* where µ is the average across the transect.

Through a vineyard management survey completed by site managers, we collected information on chemical inputs and vineyard management practices across our study sites. First, by using the reported lists of chemical inputs from each vineyard, we calculated a measure of ecotoxicity by obtaining environmental ecotoxicity information for individual active ingredients from the Pesticide and Bio-pesticide Properties Databases (Lewis *et al.*, 2016; see Supplementary material S4.3). We summed these across all active ingredients used in each vineyard to derive an overall '*Ecotoxicity score'* (calculated for 21 sites that provided the necessary information). We then multiplied each active ingredient's ecotoxicity score by its number of annual applications and summed these values to calculate an '*Ecotoxicity frequency score'* (for 17 of our sites that provided the necessary information). We rated vineyard management practices in terms of potential benefits to or detrimental impacts on biodiversity by translating evidence assessment categories from the Conservation Evidence database (ConservationEvidence.com, 2023) into a score and then we summed the scores for all vineyard management practices employed to calculate a '*Practice score'* for each study site. Details are provided in Supplementary material S4.3.

We tested for collinearity between our predictors and we found a strong negative correlation between woodland and agricultural habitats cover (r(21) = -0.876, t-value = -9.305, p-value <

0.001) and strong positive correlations between: total vine area and linear wooded features (r(21) = 0.880, t-value = 9.342, p-value < 0.001), average field size and total vine area (r(21) = 0.815, t-value = 20.701, p-value < 0.001), total edge density and woodland cover (r(21) = 0.775, t-value = 16.482, p < 0.001) and only included woodland cover and average field size in subsequent landscape-scale analyses. We also found moderate correlations between the ecotoxicity score and woodland cover (r(20) = -0.417, t-value = -6.701, p < 0.001), the ecotoxicity frequency score and woodland cover (r(16) = -0.637, t-value = -11.131, p<0.001), and the practice score and linear water features (r(20) = 0.538, t-value = 9.324, p<0.001), but retained all variables in models as the correlations were below 0.7, thus unlikely to distort model estimations (Dormann *et al.*, 2013).

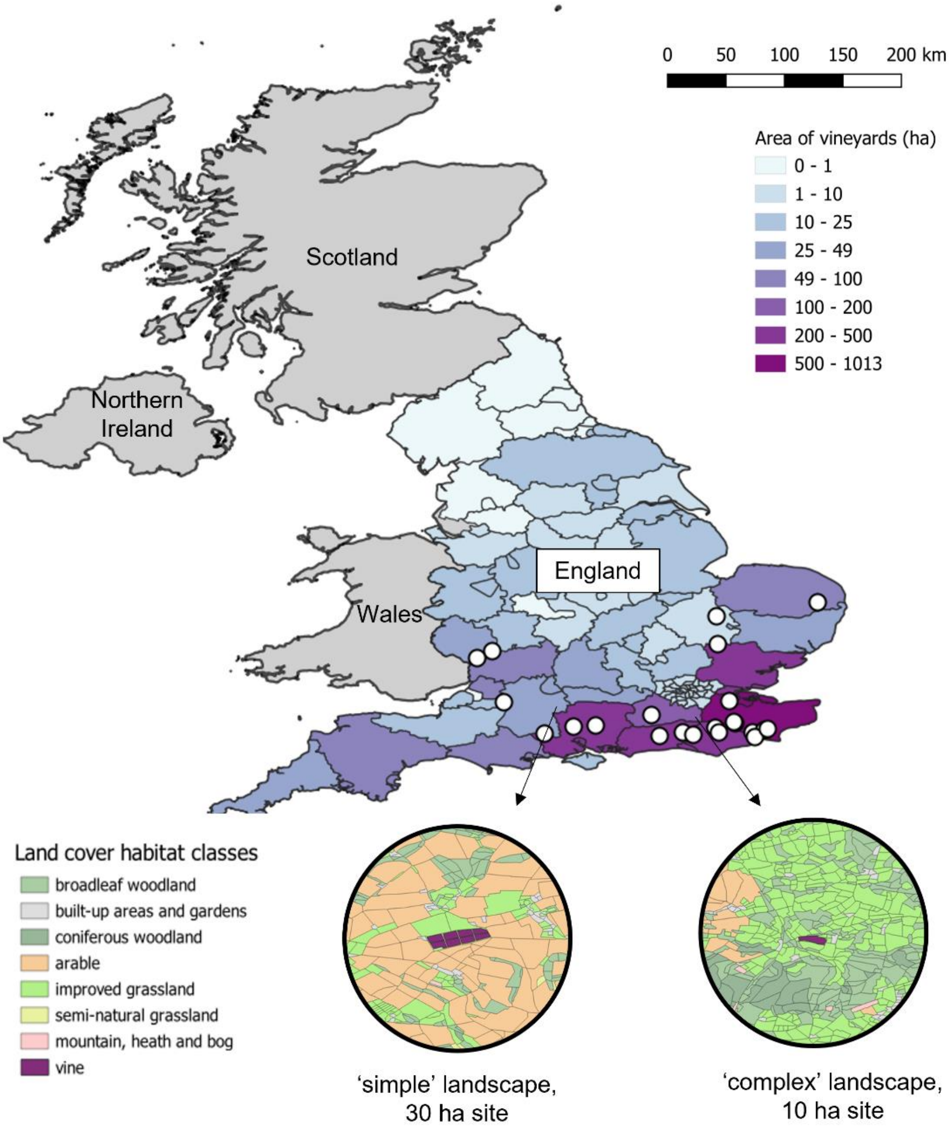


Figure 4.1. Map of the UK showing the area, in hectares, of commercial vineyards per county in England. White circles indicate study sites. Examples of two 2.5 km landscape buffers from contrasting landscapes are shown. Hectarage data were from EnglishWine.com, compiled by Stephen Skelton.

4.2.4. Data analyses

Response variables

For birds, the response variables were: abundance, species richness and Shannon diversity. We calculated these separately for each point count location and survey across the sampling periods (n=222). All observed species were included in analyses, including non-native species such as Common pheasant (*Phasianus colchicus*), due to their potential role in contributing to vineyard functions such as pest control or grape damage (anecdotal reports from vineyard managers).

For arthropods, the response variables were total abundance, and for samples containing individuals from more than one order (n=813), we calculated order Shannon diversity. We calculated these for each pitfall trap separately across all sampling locations and periods (n=1,679).

Models

We performed a set of general(ized) linear mixed models (GLMMs) to test the relative effects of habitat characteristics and vineyard management on bird and arthropod biodiversity. All analyses were performed in R 4.3.0 (R Core Team, 2021), and all models were fitted using the *spaMM* package (Rousset, 2018) with the inclusion of a spatial Matérn autocorrelation term (latitude and longitude of survey locations) as a random effect that accounted for spatial autocorrelation between our survey locations (Rousset & Ferdy, 2014).

Firstly, we related each of the five response variables described above to certified organic and SWGB-accreditation statuses. Secondly, we related each response variable to the habitat and management predictors described above, including an interaction between ground vegetation cover and season to account for vegetation cover varying across the sampling seasons. These models were repeated for predictors calculated at the landscape and local scales. All models also included survey season and year as fixed effects to account for temporal non-independence of samples.

The normality of residuals was tested using Shapiro-Wilk tests, and Gaussian error distributions were employed in models with normally distributed residuals, which included all bird models. Arthropod data were zero-inflated and therefore we performed hurdle models for these responses, which is a two-step modelling approach consisting of a presence-absence model followed by a truncated model excluding zeros (Potts & Elith, 2006). The presence-absence model was fitted using a binomial error distribution with a *clog* link function. The arthropod abundance truncated model was fitted using a negative binomial error distribution as this could not be normalised through transformation and showed overdispersion with a Poisson distribution, whereas arthropod order Shannon diversity met assumptions of normality and was therefore fitted using a Gaussian distribution. For the arthropod abundance model, we removed one outlier, where arthropod abundance was over double the next highest value, and 91% of individuals were ants, likely indicating a nearby nest. Model outputs with the retained outlier are reported in Supplementary material S4.6.

Finally, given the influence of ground vegetation cover on bird and arthropod diversity (see sections 4.3.), we fitted a Gaussian GLM with ground vegetation cover (logged term) as a response variable, and mowing and cultivation frequency per year, herbicide use, sowing of cover crops or wildflower mixes and average field size as predictors.

We used full models, interpreting predictor significance based on whether the model estimates with 95% confidence intervals passed zero, and if $p < 0.05$. We inspected the distribution of residuals, dispersion and checked for influential points using the *DHARMa* package (Hartig, 2022). All response and predictor variables, model structure, error terms and link functions are summarised in Supplementary material S4.4.

4.3. Results

4.3.1. Birds

Across 222-point count surveys, we recorded 6,853 individuals belonging to 61 species, including 15 Red-listed species of conservation concern in the UK (Stanbury *et al.*, 2021; see species list in Supplementary materials S4.5.). Bird abundance (GLMM: t-value=-0.691, p>0.05), species richness (t-value=-0.751, p>0.05) and Shannon diversity (t-value = 0.157, p>0.05) did not significantly vary between organic and non-organic sites (Figure 4.2a). Bird species richness (t-value=-2.196, p=0.036) and Shannon diversity (t-value=-2.631, p=0.012) were significantly lower at SWGB-accredited than non-SWGB vineyards, but there was no significant difference in bird abundance (t-value=-0.723, p>0.05; Figure 4.2a). Bird abundance, species richness and Shannon diversity were significantly higher at harvest than at budding, and species richness was also significantly lower in 2022 (Figure 4.2a).

At both scales, ground vegetation cover had a significant positive effect on Shannon diversity (landscape-scale GLMM model: t=2.010, p=0.026; local-scale model: t=1.866, p=0.01; Figure 4.3a-b). Model predicted Shannon diversity was 1.5 and 1.2-fold higher in vineyards with the highest vegetation cover compared to those with the lowest cover at the landscape (Figure 4.4a) and local-scales (Figure 4.4c), respectively. Ground vegetation cover did not have a significant effect on bird abundance or species richness (Figure 4.3).

At the landscape scale, Shannon diversity declined significantly with increasing ecotoxicity score (t=-2.662, p=0.019; Figure 4.3a). Model predicted Shannon diversity was 11% higher in vineyards with the lowest ecotoxicity score, compared to at vineyards with the highest ecotoxicity score (Figure 4.4b). The ecotoxicity score did not have a significant effect on bird abundance or species richness (Figure 4.3).

Vine cover at the local scale had a significant negative effect on Shannon diversity (Figures 4.3b, 4d), and the predicted Shannon diversity was 13% lower at point count locations surrounded by the highest vine cover in the study (85%) compared to the lowest (10%). Other habitat predictors did not have a significant effect on bird abundance and diversity (Figure 4.3).

4.3.2. Arthropods

Across 1,679 pitfall traps, we caught 8,726 individuals belonging to 19 orders, with the most abundant orders being Araneae (n=2,155), Coleoptera (n=2,045) and Hymenoptera (n=1,867; see Supplementary materials S4.5 for full list). Arthropod abundance was significantly higher at certified-organic than non-organic sites (GLMM: t=2.354, p=0.024, Figure 4.2b), but order Shannon diversity did not differ significantly (t=1.251, p>0.05; Figure 4.2b). There were no significant differences in arthropod abundance (t=-0.315, p>0.05), nor Shannon diversity (t=-0.789, p>0.05; Figure 4.2b) between SWGB-accredited and non-SWGB sites.

Arthropods were caught in 59% of the traps (988/1,679), and the probability of arthropod presence was significantly higher in the flowering (t=5.296, p<0.001) and harvest seasons (t=7.189, p<0.001), compared to the budding season, and was significantly lower in 2022 compared to 2021 (t=-5.697, p<0.001; Figure 4.2b).

The probability of arthropod presence decreased away from the field edge (t=-3.311, p<0.001), whilst practice score (t=5.558, p<0.001) and ground vegetation cover (t=5.523, p<0.001) had a significant positive effect (Figures 5.5a, 6a-c). Practice score also had a significant positive effect on arthropod abundance (t=2.439, p=0.015, Figure 4.5b), with predicted abundance 29% higher at vineyards with the highest practice score compared to sites with the lowest score (Figure 4.6g). Ground vegetation cover had a significant positive effect on arthropod abundance (landscape-scale: t=2.217, p=0.033; local-scale: t=4.717, p<0.001) and Shannon diversity (landscape-scale: t=2.610, p<0.001; local-scale: t=6.067, p<0.001; Figure 4.5b-c). The predicted arthropod abundance was 33% higher at the highest vegetation cover compared to the lowest cover (Figure 4.6d-e), whilst the predicted Shannon diversity increased by 50% (Figure 4.6h-i).

Ecotoxicity score had a significant negative effect on arthropod abundance (t=--2.026, p=0.043) and Shannon diversity (t=-2.415, p<0.001), whilst ecotoxicity frequency score had a significant negative effect on Shannon diversity (t=-3.987, p<0.001, Figure 4.5b). Predicted arthropod abundance and Shannon diversity in vineyards with lowest ecotoxicity score were 12% and 10% higher, respectively, than in vineyards with highest ecotoxicity score (Figure 4.6f and j), whilst the predicted Shannon diversity reduced by 38% in vineyards with the highest ecotoxicity frequency score compared to those with the lowest score (Figure 4.6k).

4.3.3. Differences between vineyards

Ecotoxicity scores were significantly lower for certified-organic (12.33 ± 2.69 SE) than for non-organic vineyards (33.17 ± 2.69; t(19)=-4.758, p<0.001; Figure 4.7a), whilst the ecotoxicity score was significantly lower at non-SWGB (17.20 ± 2.78) than SWGB-accredited vineyards (30.64 ± 4.74; t(19)=2.385, p<0.05; Figure 4.7b). The ecotoxicity frequency scores did not vary based on vineyard management (certified-organic vs non-organic: t(15)=0.005, p-value>0.05; SWGB-accredited vs non-SWGB: t(15)=1.319, p-value>0.05).

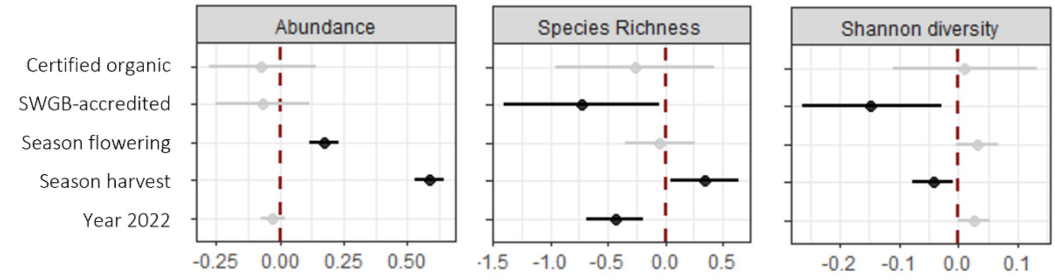
The practice scores were significantly higher at non-SWGB than at SWGB-accredited vineyards (0.89 ± 0.82 and -1.25 ± 0.66 respectively; t(19)=2.040 , p>0.05; Figure 4.7d), but did not vary between certified-organic and non-organic vineyards (non-organic: -1.45 ± 0.74; certified-organic: 0.90 ± 0.67; t(19)=1.823, p-value>0.05; Figure 4.7c). There were no significant differences between vineyards under different management in mowing (certified-organic vs. non-organic: t(19)=-0.265, p<0.05; SWGB-accredited vs. non-SWGB: t(19)=0.087, p>0.05), cultivation frequency (certified-organic vs. non-organic: t(19)=-1.170, p>0.05; SWGB-accredited vs. non-SWGB: t(19)=1.748, p>0.05), or overall ground vegetation cover (certified-organic vs.

non-organic: t(19)=0.974, p-value>0.05; SWGB-accredited vs. non-SWGB: t(19)=-0.804, p-value>0.05; see Supplementary materials S4.7. for details).

Ground vegetation cover was significantly higher in vineyards that did not use herbicides than those that did (t=2.760, p=0.015), and it significantly decreased with field size (t=-2.784, p=0.014; Figures 4.8a-c).

Full model results are reported in Supplementary materials S4.6.

(a) Birds



(b) Arthropods

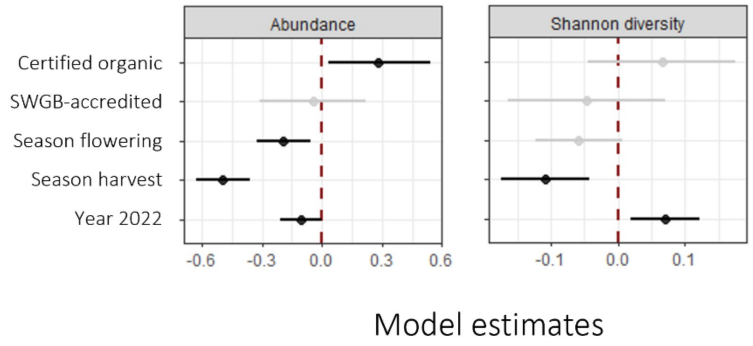
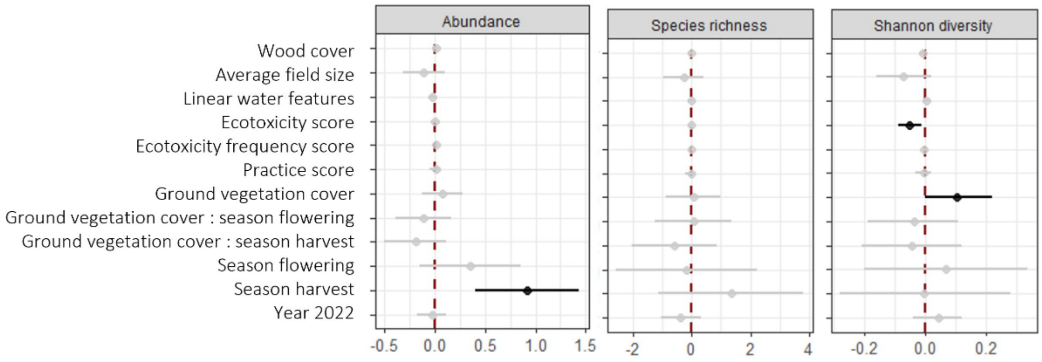


*Figure 4.2. Estimates and 95% confidence intervals from GLMMs comparing bird **(a)** and arthropod **(b)** response variables between vineyards (n=22) accredited through different schemes. For birds, the modelled response variables were: abundance (marginal R^2=0.42), species richness (R^2=0.16) and Shannon diversity (R^2=0.27); for arthropods, the response variables were: abundance (R^2=0.20) and order Shannon diversity (R^2=0.12).* Estimates in black indicate predictors with supported effects (95% CI do not cross zero, and p<0.05).

(a) landscape-scale



(b) local-scale (200 m around point count)

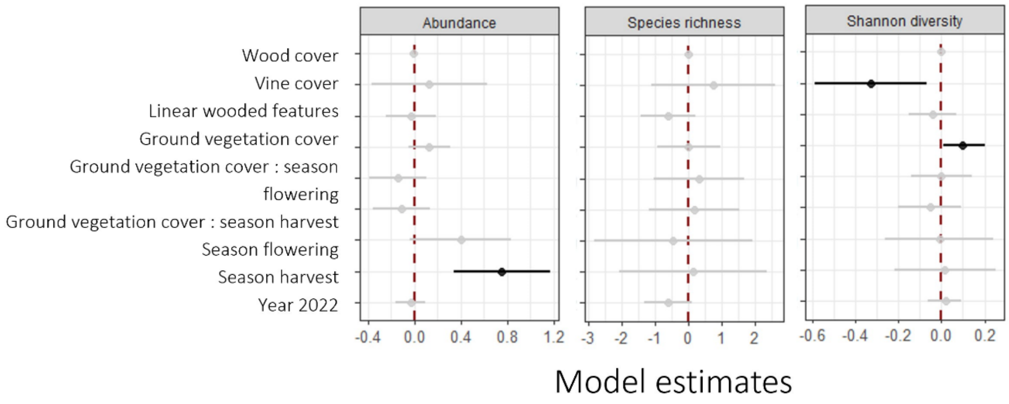


Figure 4.3. Estimates and 95% confidence intervals from GLMMs at **(a)** the landscape-scale (2.5 km buffer around each site, n=22), and **(b)** the local-scale (200 m buffer around each point count survey, n=44) for the effects of habitat and management predictors on bird abundance (marginal R^2 = 0.46 at landscape scale, R^2 = 0.27 at local scale), species richness (R^2 = 0.35 and 0.03, respectively), and Shannon diversity (R^2 = 0.63 and 0.16, respectively). Estimates in black indicate predictors with supported effects (95% CI do not cross zero, and $p<0.05$).

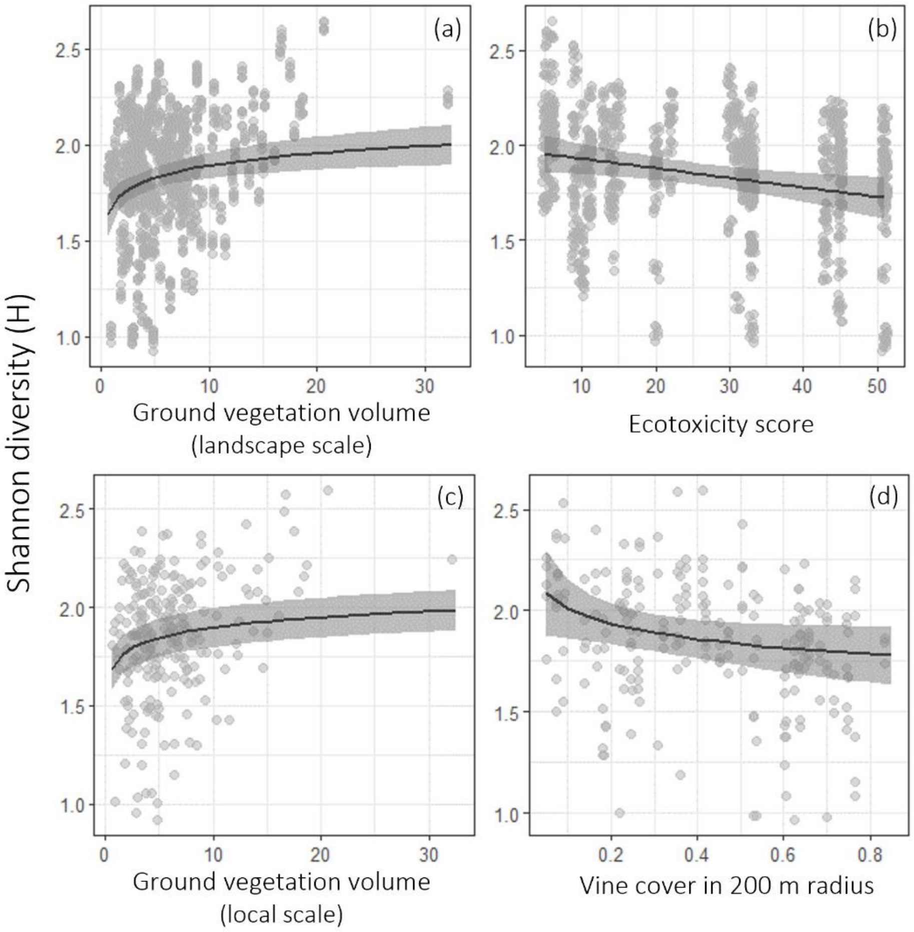
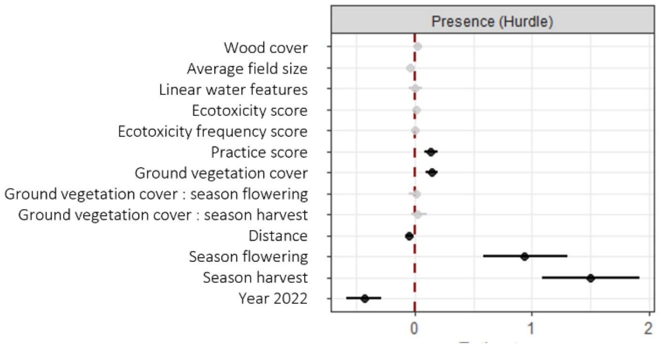
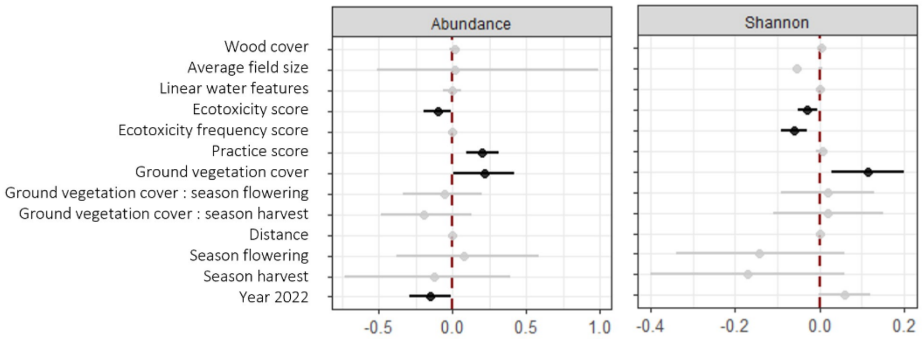


Figure 4.4. Raw (circles, n=222) bird Shannon diversity in relation to significant predictors, with model predictions (black line with 95% confidence intervals in grey). Landscape scale refers to 2.5 km buffer around vineyards (n=22, **a-b**), and local scale to 200 m buffer around point count locations (n=44**, c-d)**.

(a) Presence-absence at landscape scale



(b) landscape-scale



(c) local-scale (100m around transect)

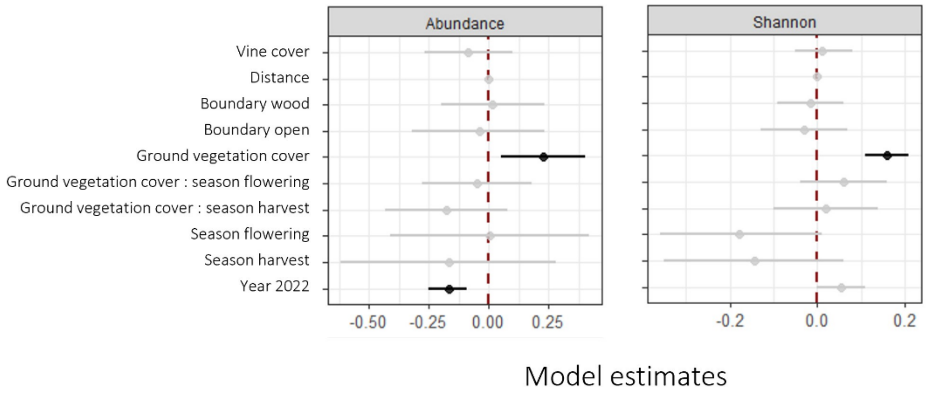


Figure 4.5. Estimates and 95% confidence intervals from hurdle GLMMs at **(a, b)** the landscape-scale (2.5 km buffer around each site, n=22), and **(c)** the local-scale (100 m buffer around each transect, n=79) for the effects of habitat and management predictors on arthropod presence (**a,** marginal $R^2 = 0.31$), abundance ($R^2 = 0.56$ at the landscape, $R^2 = 0.18$ at the local-scale) and order Shannon diversity ($R^2 = 0.19$ and $R^2 = 0.15$, respectively; **b, c**). Estimates in black indicate predictors with supported effects (95% CI do not cross zero, and p<0.05).

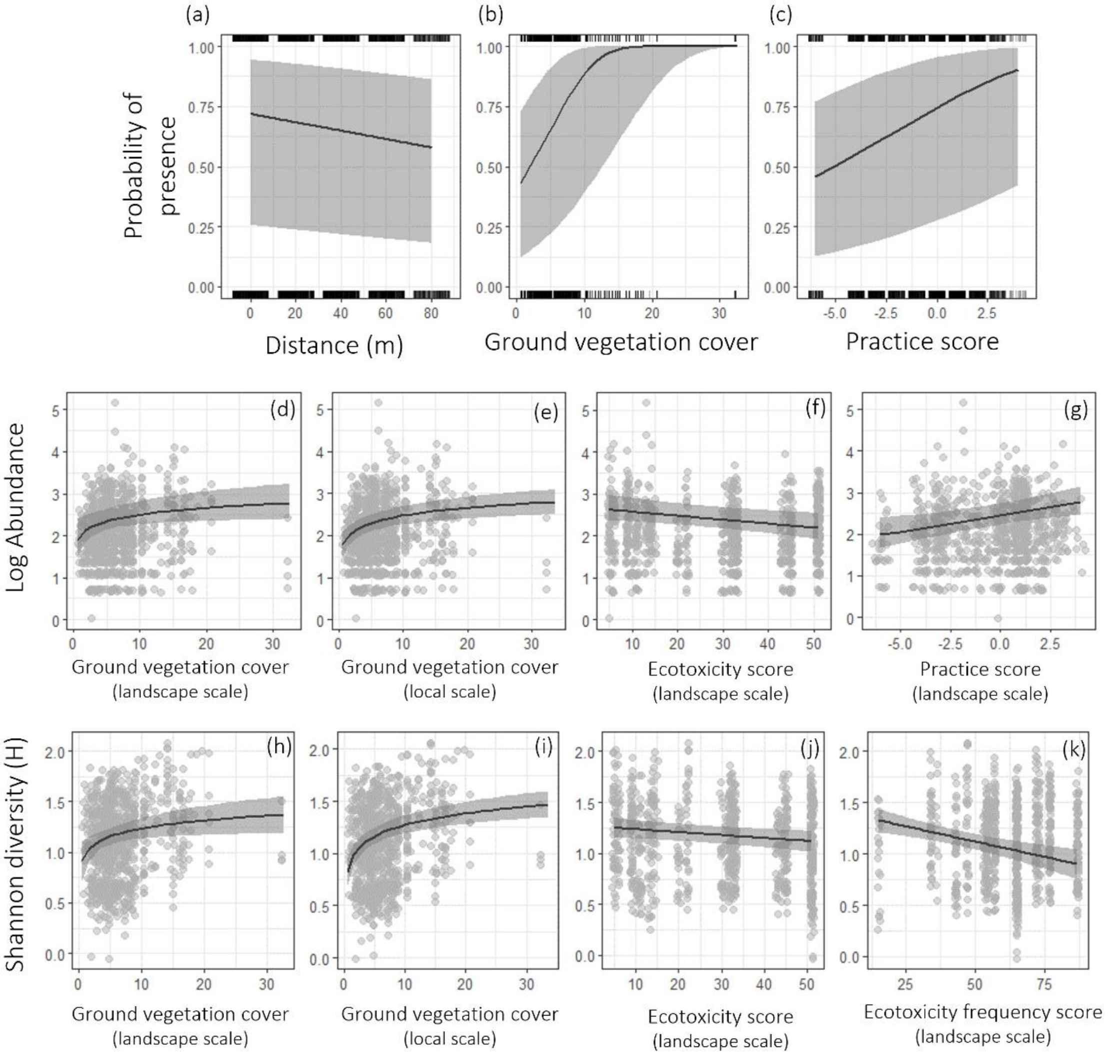


Figure 4.6. Raw (circles) arthropod occurrence **(a-c)**, abundance (**d-g)** and order-level Shannon diversity **(h-k)** in relation to significant predictors with model predictions (black line with 95% confidence intervals in grey). Landscape scale refers to 2.5km buffer around vineyards (n=22), and local scale to 100m buffer around transects (n=79).

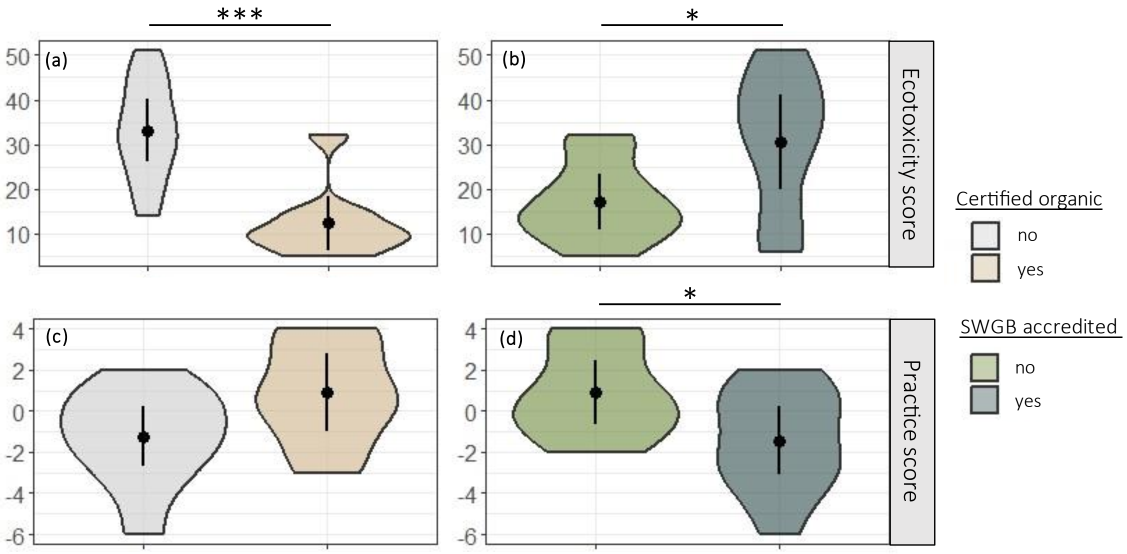


Figure 4.7. Comparison of ecotoxicity **(a-b)** and practice scores **(c-d)** between vineyards that were certified organic (n=10/22) and non-certified organic **(a and c)**, as well as those that were Sustainable Wines of Great Britain (SWGB) accredited (n=11/22) and those without the accreditation **(b and d)**. The mean and 95% confidence intervals are indicated in black. Significance of differences was tested with two-sample t-tests and significant results are indicated with asterisks (* p<0.05, *** p<0.001).

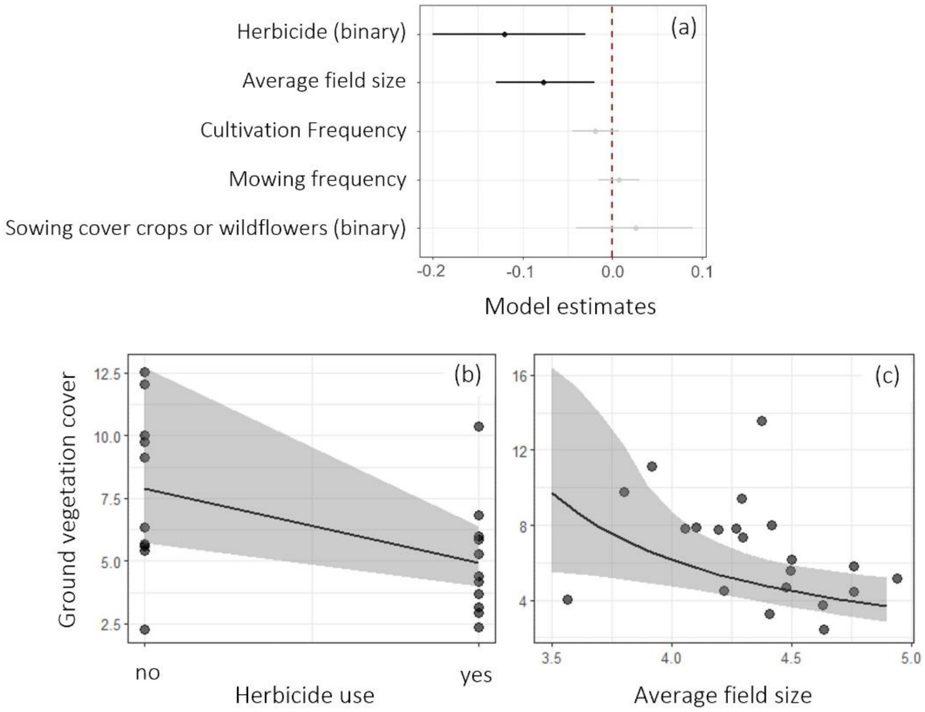


Figure 4.8. Estimates and 95% confidence intervals from a GLM relating ground vegetation cover to predictors (marginal R^2=0.76, **a**) across our study vineyards (n=22), and the raw values (circles) and model predictions in black line with 95% confidence intervals in grey for significant predictors **(b,c)**.

4.4. Discussion

We found vineyard management practices, rather than the surrounding semi-natural habitats, to be the key drivers of differences in bird and arthropod biodiversity across English vineyards. We show that neither organic certification nor a wine industry sustainability accreditation scheme are currently indicative of higher biodiversity, as the only positive impact on vineyard biodiversity was seen for arthropod abundance in organic vineyards, whilst we found lower bird diversity in SWGB-accredited vineyards. Across Europe, mixed effects of organic viticulture on bird diversity have been noted, as some studies, like us, failed to detect an effect (Assandri *et al.*, 2016, 2017), whilst others reported positive effects (Barbaro *et al.*, 2021; Puig-Montserrat *et al.*, 2017; Rollan *et al.*, 2019). We may have found stronger effects if we included plant diversity in our comparisons, as plants have been shown to benefit from organic viticulture more than mobile organisms (Assandri *et al.*, 2016; Fuller *et al.*, 2005; Ostandie *et al.*, 2021). Furthermore, the benefits resulting from organic, or otherwise sustainable management, may be stronger in landscapes that are more homogenous and intensively managed than those in our study (Rollan *et al.*, 2019; Tuck *et al.*, 2014). The species found across English vineyard landscapes may also be generalists and less sensitive to farming and management practices, as much farmland biodiversity across lowland England has been strongly altered since mid-20th Century by agricultural intensification (Robinson & Sutherland, 2002).

SWGB-accredited vineyards had significantly higher ecotoxicity scores, which were negatively related to bird and arthropod diversity, and arthropod abundance. A direct negative effect of insecticide and fungicide use on biodiversity was previously demonstrated across European farmland (Geiger *et al.*, 2010; Rigal *et al.*, 2023). Whilst organic vineyards used fewer chemicals, which resulted in significantly lower ecotoxicity scores, the frequency with which chemicals were applied was higher, leading to the ecotoxicity frequency score not differing significantly between organic and non-organic sites. This is an important distinction as frequency of agrochemical application is also important (Geiger *et al.*, 2010), and we found the ecotoxicity frequency score to have a stronger negative effect on arthropod diversity than the ecotoxicity score alone. Thus, organic management without efforts to minimise application frequency may not be sufficient to support biodiversity on farms, especially as organically certified agrochemicals such as copper have serious consequences for biodiversity and microbial activity in vineyards (Karimi *et al.*, 2021). A caveat to these observations is the crudeness of the ecotoxicity measurements used to calculate our ecotoxicity scores. Responses of organisms to agrochemicals depend on environmental factors beyond those tested in laboratory studies on which ecotoxicity measures are based (Chapman *et al.*, 1998; Niederlehner *et al.*, 1990), whilst synergistic and antagonistic interactions of different agrochemicals co-applied at a given farm are largely unknown (Hernández *et al.*, 2017).

In line with previous vineyard research (Paiola *et al.*, 2020; Winter *et al.*, 2018), we found strong positive effects of ground vegetation cover on biodiversity. This is not surprising as ground vegetation provides shelter and more stable conditions for invertebrates, and food for both invertebrates and birds (Arlettaz *et al.*, 2012; Winter *et al.*, 2018). We found herbicide applications to decrease vegetation cover, whilst increasing a site's ecotoxicity score, and detrimental effects of herbicide use on biodiversity have been shown in other European vineyards (Duarte *et al.*, 2014; Nascimbene *et al.*, 2012; Winter *et al.*, 2018). Ground vegetation cover was also lower in vineyards with larger fields, which may be related to more intensive management methods, such as the use of heavier machinery and increased ground disturbance and trampling by vineyard workers (Cabodevilla *et al.*, 2021).

Vine cover reduced Shannon diversity of the bird community at the local scale, supporting the observed negative effect of increasing vine cover in other European vineyards (Pithon *et al.*, 2016; Rösch *et al.*, 2023). This is likely because alternative surrounding habitats, such as hedgerows and woodland patches that are abundant across English vineyards and were chosen as nesting sites across German vineyards (Rösch *et al.*, 2023), provide better habitats for birds. These habitats may also be important for supporting arthropod communities, as arthropod presence decreased away from field edges. However, contrary to previous findings and our predictions (Barbaro *et al.*, 2021; Paiola *et al.*, 2020; Rösch *et al.*, 2023), we found no other effects of surrounding semi-natural habitat area on vineyard biodiversity. This could be because we measured these effects at larger spatial scales than those considered by other studies (e.g. Rösch *et al.*, 2023), or that the species inhabiting English vineyards may be generalists and well-adapted to agricultural conditions, as shown in previous research for birds (Robinson & Sutherland, 2002) and arthropods (Geldenhuys *et al.*, 2022), and thus may be less reliant on the surrounding habitats.

4.5. Synthesis, management and policy implications

Across English vineyards, we found that individual management practices had a stronger influence on vineyard biodiversity than the overall management regime or the surrounding habitats. Our research demonstrates the importance of looking beyond farming certifications or industry-accreditations, as these may not reliably predict higher biodiversity. We identified key drivers of biodiversity in vineyards, which we use to make management recommendations for supporting biodiversity. Firstly, the types of agrochemicals used, and the frequency of application should be carefully managed to reduce detrimental impacts. Moving to organic management alone may not achieve this, as agrochemicals permitted within organic certifications, for example copper, can both have high ecotoxicity scores and lower efficacy, thus requiring repeated applications. Instead, vineyard managers should be encouraged to consult the open-access PBPD database (Lewis *et al.*, 2016) to assess the environmental ecotoxicity scores and opt for chemicals with lower scores, a strategy already shown to benefit arthropod diversity in South African vineyards (Geldenhuys *et al.*, 2022). Reducing or eliminating the use of herbicides, which have high environmental ecotoxicity and reduce vegetation cover, is also key to supporting biodiversity within vineyards. The second recommendation is to increase vegetation cover in vineyards.

Ground vegetation can be diversified and its cover increased by sowing cover crops and wildflowers, which has been shown to effectively increase biodiversity in vineyards, and yield further benefits through enhanced natural pest control (Brambilla & Gatti, 2022; Griffiths-Lee *et al.*, 2023; Winter *et al.*, 2018).

The English viticultural industry has a strong focus on sustainability, evidenced by the wide uptake of the SWGB-accreditation. However, we found SWGB-accredited vineyards to host lower bird diversity, and have higher ecotoxicity scores than non-accredited vineyards, and therefore at present the scheme's accreditation does not appear to be indicative of higher biodiversity or the use of management practices expected to be positive for biodiversity. This does not undermine the value of the scheme, which only started in 2020, as members commit to continual improvement and annual reporting of management across many areas, including biodiversity conservation. However, this also showcases the importance of studying and identifying the drivers of biodiversity across novel agro-ecosystems to enable accreditation schemes to make evidence-based recommendations and set minimal requirements that ensure their objectives are realised.

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Chapter 4 – Supplementary Materials

S4.1. Bird and arthropod sampling diagram

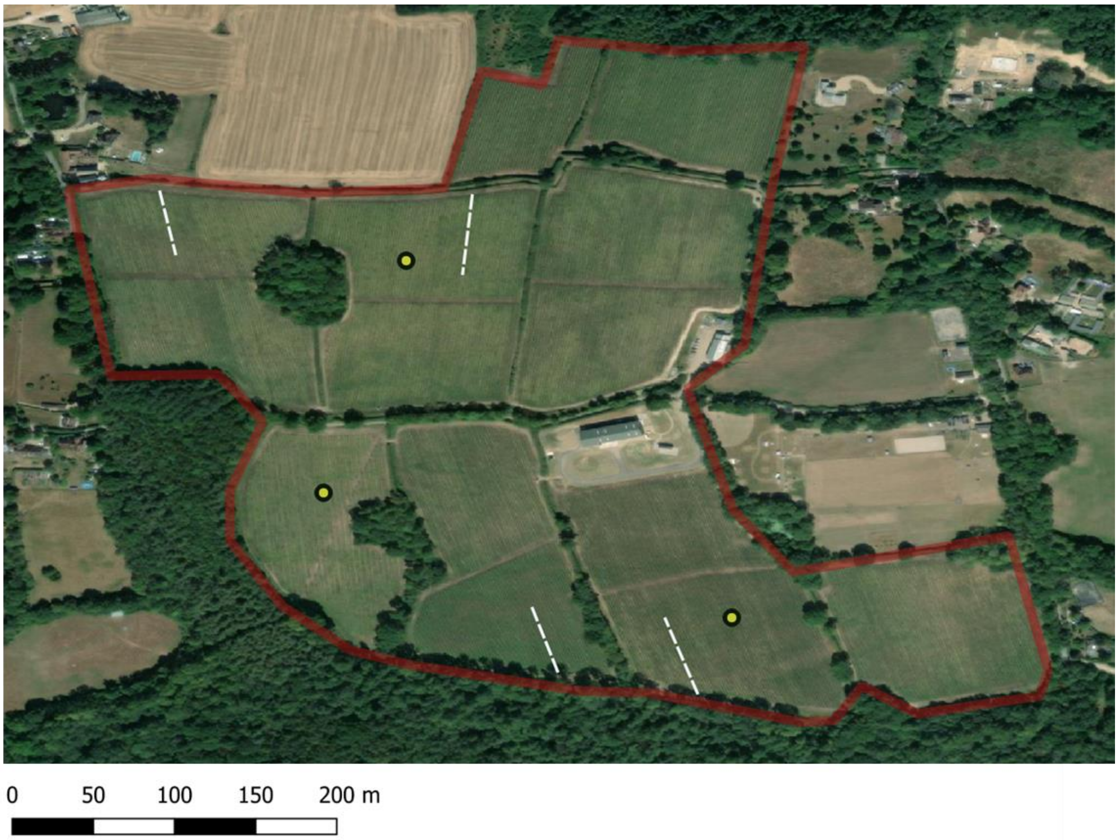


Figure S4.1. Map of an example study site showing the sampling design across a whole vineyard with a yellow circle indicating locations of bird point count surveys, and white dashed lines indicated transect locations were pitfall traps were set up, and ground vegetation cover and height was measured. The outer boundary of the vineyard is shown in red. This is an example of a non-organic 60 ha site.

S4.2. Ground vegetation cover across English vineyards

Figure S4.2. Examples of vineyard floors across our research study sites. Ground vegetation management varied greatly across the study sites and sampling periods with different intensities of mowing, cultivation and herbicide use. Some vineyards had complete floor cover (**a**), though it was common that the alleyways between grapevine rows had cover and a 40-60 cm strip directly underneath the grapevines was left bare (**b, c** and **f**). Some vineyards had minimal ground cover (**e**). The ground vegetation in the strip underneath grapevines was mostly managed by cultivation (**b** and **c**), though some vineyards applied herbicides (**f**). Grasses were the dominant cover type (e.g. **a** and **b**), though forbs dominated in some vineyards (**g**). Sward height was highest mid-season (flowering) when sowed flower mixes were also evident in some vineyards (**d**).

S4.3. Ecotoxicity, ecotoxicity frequency and practice scores

We used a questionnaire aimed at vineyard managers to collect information on chemical use and input-frequency, as well as on the use of a set of vineyard management practices and their frequency. The questionnaire was part-filled by 21/22 vineyard managers, and fully completed by 17. Based on the responses, we calculated three management scores: *ecotoxicity score, ecotoxicity frequency score and practice score.*

Ethical approval for the questionnaire was obtained from the Faculty of Science Research Ethics Subcommittee at the University of East Anglia (ETH2223-0561).

Ecotoxicity and ecotoxicity frequency scores

We used the Pesticide (PPDB) and Bio-pesticide (BPDB) Properties Databases (Lewis *et al.* 2016) from the University of Hertfordshire to calculate an ecotoxicity score for each site based on the chemical use information. The databases are a comprehensive source of data on the chemical, physical and biological properties of fungicides, herbicides and insecticides used in (Lewis *et al.* 2016, Lewis & Tzilivakis 2017). For each chemical, the database provides an 'Ecotoxicity' rating of 'Low', 'Moderate' or 'High'. This rating is an aggregate of terrestrial ecotoxicity scores under different categories, such as LD_{50} (doses required to kill half the test population), and LC_{50} (concentrations required to kill half the test population) values, and chronic effects (the consequences of chemical exposure that arise slowly and are long-lasting and irreversible), across multiple taxa, including mammals, birds, earthworms, collembola and pollinators. The database provides a 'Low', 'Moderate' and 'High' rating for each of these metrics and taxa, as permitted by data availability, and the rating is based on 'rule of thumb' thresholds to provide a simple comparison, with the caveat that these ratings should be treated with caution as they are simplistic, based on varied amount of scientific evidence and take no account of factors that may affect ecotoxicity, such as aquatic solubility or mode of application.

We graded the aggregate ecotoxicity scores for each chemical used by our study sites as follows: 'Low' scored 1, 'Moderate' scored 2 and 'High' scored 3 (see Table S4.3.1 for a list of chemicals). The sum of these across all chemicals used by a vineyard gave a single sum per site, termed '*site ecotoxicity score*'. Using information on application frequency per vineyard, we multiplied the ecotoxicity score by the number of applications per year. For example, if a chemical with 'Moderate' ecotoxicity rating was applied three times a year, the resulting ecotoxicity score for that chemical at a site was 6. We summed these ‘frequency scores’ per site to get a single sum termed ‘*site ecotoxicity frequency score*’.

We performed this for all sites that we had information available for, which was 21 for *‘site ecotoxicity score’* and 17 for ‘*site ecotoxicity frequency score*’.

Table S4.3.1. List of agrochemicals used across our study sites (n=21), including information of their use, ratings of ecotoxicity from the Pesticide (PPDB) and Bio-pesticide (BPDB) Properties Databases (Lewis *et al.* 2016), and indicating whether they were used within certified organic vineyards.

Name	Use	Active ingredient	ecotoxicity	Used in certified-organic?
Amylo X WG	powdery mildew, botrytis	bacillus amyloliquefaciens plantarum D747	low	Yes
Botector	botrytis	Aureobasidium pullulans	low	Yes
Calcium	fertiliser	calcium	low	Yes
Copper	fungicide, downy mildew	copper sulfate	high	Yes
Cosine	powdery mildew	cyflufenamid 50g/L	high	No
DiPel DF	insecticide	bacillus thuringiensis kurstaki ABTS-351	moderate	No
Filan	fungicide	50% w/w boscalid	moderate	No
Frutogard	downy mildew	342 g/L potassium phosphate	moderate	No
Fusilade Max	herbicide	125 g/l fluazifop-p-butyl	moderate	No
Fytosave	powdery mildew	12.500 g / l COS-OGA (chitooligosaccharides / oligogalacturonides)	no data	Yes
Iron	fertiliser	iron	high	Yes
Justice	powdery mildew	200 g/litre proquinazid	high	No
Karma	botrytis	850 g/Kg potassium hydrogen carbonate	moderate	No
Magnesium	fertiliser	Magnesium phosphide	high	Yes
Manganese	fertiliser	NA	no data	Yes
Nativo 75WG	fungicide	500 g/kg tebuconazole	high	No
Nativo 75WG	fungicide	250 g/kg trifloxystrobin	high	No
Option	fungicide	600g/kg cymoxanil	moderate	No
Percos	fungicide	300g/L ametoctradin	high	No
Percos	fungicide	225g/L dimethomorph	high	No
Potassium bicarbonate	powdery mildew	Potassium bicarbonate	moderate	Yes
Prolectus	fungicide, botrytis	fenpyrazamine	moderate	No

Romeo	fungicide	941 g/kg of Cerevisane	low	Yes
Roundup Powermaxx*	herbicide	72% w/w glyphosate	moderate	No
Scala	fungicide	400 g/l pyrimethanil	moderate	No
Sercadis	powdery mildew, botrytis	300 g/l fluxapyroxad	high	No
Serenade ASO	fungicide	1015.1 g/L Bacillus subtilis strain QST 713	low	Yes
Shark	herbicide	60 g/L carfentrazone-ethyl	moderate	No
Shinkon	fungicide	200 g / l amisulbrom	high	No
SL567a	fungicide	465.2 g/l metalaxyl-M	moderate	No
Steward	pollen beetle, insecticide	300 g/ kg indoxacarb	high	No
Stroby WG	fungicide	50% w/w kresoxim-methyl	high	No
Sulfur	powdery mildew	sulfur	no data	Yes
Switch	fungicide	37.5% w/w cyprodinil	high	No
Switch	fungicide	25% w/w fludioxonil	high	No
Systhane 20EW	fungicide	103 g/litre cyclohexanone	low	No
Systhane 20EW	fungicide	200 g/litre myclobutanil	moderate	No
Teldor	fungicide, botrytis	50% w/w fenhexamid	moderate	No
Topas	powdery mildew	penconazole	moderate	No
Valbon	fungicide	17.5 g/kg benthiavalicarb-isopropyl	moderate	No
Valbon	fungicide	700 g/kg mancozeb	high	No
Vintec	fungicide	Trichoderma atroviride SC1 1×1013	low	No
Vivando	fungicide, cobweb mould	500 g/l metrafenone	moderate	No
Zinc	fertiliser	zinc	no data	Yes

Practice score

We used conservation action assessments from the Conservation Evidence database (ConservationEvidence.com, 2023) to rate the habitat management practices performed by the study vineyards. Conservation Evidence effectiveness scores are based on judgement from a panel of independent experts on whether an action is likely to be effective or not. This assessment is based on expert knowledge and by judging the quality of available evidence linked to that action (Sutherland *et al.* 2021). We used the effectiveness categories from Conservation Evidence to score the practices undertaken across our sites as described in Table S4.3.2.

We scored the effectiveness categories from Conservation Evidence as follows: 'Beneficial' = 2, 'Likely to be beneficial' = 1, 'Trade-offs between benefits & harms' and 'Unknown effectiveness' = 0, 'Unlikely to be beneficial' = -1, 'Likely to be ineffective or harmful' = -2. In cases where the opposite action to the Conservation Evidence action was performed, we reversed the scoring. For example, if the conservation action of 'not-mowing' had an effectiveness category of 'Beneficial', we scored 'mowing' as the equivalent of 'Likely to be ineffective or harmful'. For some of the practices, we also considered their spatial extent and separately added the practice score for each additional spatial area that the practice in question was performed. This applied to mowing, cultivation and sowing of wildflowers, which could have been performed in all or any of: under vine, in the alleyways and headlands. For example, if cultivation was performed under vine, in alleyways and headlands, then the score for the action of cultivation would be added three times. We summed the effectiveness scores for all practices that were performed at each site to get a single sum per site, termed '*site practice score*'.

Reference list

Bladon, Andrew J., Smith, Rebecca K., Sutherland, William J. 2022. *Butterfly and Moth Conservation Global evidence for the effects of interventions for butterflies and moths*. University of Cambridge, Cambridge, UK.

Dicks, L.V., Ashpole, J.E., Dänhardt, J., James, K., Jönsson, A., *et al.* 2013. *Farmland Conservation: Evidence for the effects of interventions in Northern Europe*. Pelagic Publishing, Exeter.

Lewis, K. & Tzilivakis, J. 2017. Development of a Data Set of Pesticide Dissipation Rates in/on Various Plant Matrices for the Pesticide Properties Database (PPDB). *Data* 2: 28.

Lewis, K.A., Tzilivakis, J., Warner, D.J. & Green, A. 2016. An international database for pesticide risk assessments and management. *Human and Ecological Risk Assessment: An International Journal* 22: 1050–1064.

Sutherland, W.J., Dicks, L.V., Petrovan, S.O. & Smith, R.K. 2021. *What Works in Conservation: 2021*. Open Book Publishers.

Table S4.3.2. List of management practices performed in the study vineyards and the effectiveness category of the most relevant practice from Conservation Evidence (www.conservationevidence.com, Sutherland *et al.* 2021), along with the practice scores we assigned and that were used to calculate an overall 'site practice score'. Our practice scores were assigned as follows: Conservation Evidence category 'Beneficial' = 2, 'likely to be beneficial' = 1, 'Trade-offs between benefits & harms' and 'Unknown effectiveness' = 0, 'Unlikely to be beneficial' = -1, 'Likely to be ineffective or harmful' = -2. In cases when the vineyard management practice opposed the beneficial action described in Conservation Evidence, the scores were reversed (e.g. Reduced cultivation is categorised as '*Likely to be beneficial'* by Conservation Evidence, giving it a score of 1, so a score of -1 was added each time a vineyard site was cultivated, so cultivation twice a year would give a score of -2).

Practice	Conservation Evidence effectiveness category	Our practice score	Evidence
Mulch pruning in alleyways	*Likely to be beneficial*	1	(Dicks, *et al.* 2013)
Mowing alleyways, headlands and / or under vines	*Beneficial* 'leave uncultivated margins' *Unknown effectiveness (limited evidence)* – 'raise mowing height' *Likely to be beneficial* – 'delay mowing on pasture or grassland'	-1	(Dicks, *et al.* 2013)
Cultivate alleyways, headlands and / or under vines	*Likely to be beneficial* – 'reduce tillage'	-1	(Dicks, *et al.* 2013)
Sow wildflowers in alleyways, headlands	*Beneficial* – 'Plant nectar flower mixture / wildflower strips'	2	(Dicks, *et al.* 2013)
Sow cover crops in vineyard	*Beneficial* – 'plant wild bird seed or cover' *Awaiting assessment* – undersow with cover crops but two studies were available	2	(Dicks, *et al.* 2013, Bladon, Andrew J., Smith, Rebecca K., Sutherland, William J. 2022)
Use chemical fertiliser	*Beneficial* – 'reduce fertiliser use generally'	-2	(Dicks, *et al.* 2013)
Use natural fertiliser (e.g. manure)	*Beneficial* – 'use organic rather than mineral fertiliser' There is limited evidence of the effects of natural fertilisers vs. no fertiliser	1	(Dicks, *et al.* 2013)

S4.4. Description of response variables, predictors and model structure

Response Variables	Description	Error (and link) functions
Bird abundance (logged)	Non-negative discrete. Total number of bird individuals recorded per survey.	Gaussian (identity)
Bird species richness	Non-negative discrete. Total number of bird species recorded per survey.	Gaussian (identity)
Bird Shannon diversity	Non-negative continuous. A metric calculating the diversity of species per survey, based on abundance and species richness.	Gaussian (identity)
Arthropod presence	Binary. Presence or absence of arthropods in each pitfall trap.	Binomial (clog)
Arthropod abundance	Non-negative continuous. Total number of arthropods collected per pitfall sample.	Negative binomial (log)
Arthropod order Shannon diversity	Non-negative continuous. A metric calculating the diversity of arthropod orders per survey, based on abundance and species richness.	Gaussian (identity)
Ground vegetation cover (logged)	A measure of ground vegetation cover based on sward height and proportion of ground covered with live vegetation. See Methods for details.	Gaussian (identity)

Explanatory Variables	Description
Woodland cover	Proportional. Proportion cover by deciduous, mixed and coniferous woodland. Calculated at landscape (2.5 km buffer around each vineyard) and local (200 m buffer around point counts) scales.
Linear water features	Continuous. Length of streams and rivers in a 2.5 km landscape buffer.
Linear wooded features	Continuous. Length of hedgerows and line trees at the local scale (200 m buffer around point counts).
Ground vegetation cover	Continuous. A measure of ground vegetation cover based on sward height and proportion of ground covered by live vegetation.
Average field size	Continuous. Average size of vine field per vineyard.
Vine cover	Proportional. Proportion of local scale buffer (100 m around pitfall traps, or 200 m around point counts) covered by vines.
Ecotoxicity score	Discrete. A measure, per vineyard, of environmental toxicity from applied agrochemicals. See paper for details.
Ecotoxicity frequency score	Discrete. A measure, per vineyard, of environmental toxicity from applied agrochemicals multiplied by application frequency. See paper for details.
Practice score	Discrete. A measure, per vineyard, of how beneficial management practices are for supporting biodiversity conservation. See paper for details.
Herbicide	Binary (yes / no). Whether a vineyard applies herbicides.

Cultivation frequency	Discrete. Frequency of cultivation at a vineyard per year.
Mowing frequency	Discrete. Frequency of mowing at a vineyard per year.
Sowing cover crops or wildflowers	Binary (yes / no). Whether a vineyard sows cover crops or wildflowers within vine fields.
Boundary type	Categorical with 3 levels (hedgerow, woodland, open). Boundary edge from which arthropod sampling transects ran from.
Distance	Categorical with 3-5 levels (0, 20, 40, 60, 80 m). Distance away from boundary edge at which pitfall traps were set up.
Season	Categorical with 3 levels (budding, flowering or harvest). Sampling season.
Year	Categorical with 2 levels (2021, 2022). Sampling year.
Certified organic	Binary (yes, no). Whether a vineyard was certified organic.
SWGB-accredited	Binary (yes, no). Whether a vineyard was accredited through the Sustainable Wines of Great Britain certification scheme.

Response variable	Model structure
Bird abundance (logged)	Certified organic + SWGB-accredited + Season + Year
Bird species richness	
Bird Shannon diversity	
Bird abundance (logged)	[landscape scale] Woodland cover + Average field size + Linear water features + Ecotoxicity score + Ecotoxicity frequency score + Practice score + Ground vegetation cover + Ground vegetation cover * Season + Season + Year + Mátern spatial term
Bird species richness	
Bird Shannon diversity	
Bird abundance (logged)	[local scale] Woodland cover + Vine cover + Linear wooded features + Ground vegetation cover + Ground vegetation cover * Season + Season + Year + Mátern spatial term
Bird species richness	
Bird Shannon diversity	
Arthropod abundance	Certified organic + SWGB-accredited + Season + Year
Arthropod order Shannon diversity	
Arthropod presence	[landscape scale] Woodland cover + Average field size + Linear water features + Ecotoxicity score + Ecotoxicity frequennncy score + Practice score + Ground vegetation cover + Ground vegetation cover * Season + Distance + Season + Year + Mátern spatial term
Arthropod abundance	
Arthropod order Shannon diversity	
Arthropod abundance	[local scale] Vine cover + Boundary type + Distance + Ground vegetation cover + Ground vegetation cover * Season + Season + Year + Mátern spatial term
Arthropod order Shannon diversity	
Ground vegetation cover	Herbicide + Cultivation frequency + Mowing frequency + Average field size + Sowing cover crops or wildflowers

S4.5. Summary table of bird species and arthropod orders

Table S4.5.1. Number of individuals of bird species recorded across either certified-organic (n=10) and non-organic (n=12) vineyards, or across Sustainable Wines of Great Britain scheme (SWGB) accredited (n=11) or not accredited (n=11) vineyards. Red list status is based on Birds of Conservation Concern 2021 list.

Common species name	Latin name	Red-listed	Certified-organic	Non-organic	SWGB-accredited	non-SWGB
Barn swallow	*Hirundo rustica*	no	20	28	24	24
Black headed gull	*Chroicocephalus ridibundus*	no	16	2	0	18
Blackbird	*Turdus merula*	no	124	167	135	156
Blackcap	*Sylvia atricapilla*	no	13	13	9	17
Blue tit	*Cyanistes caeruleus*	no	84	113	77	120
Buzzard	*Buteo buteo*	no	15	39	31	23
Canada geese	*Branta canadensis*	no	52	8	14	46
Carrion crow	*Corvus corone*	no	302	643	538	407
Chaffinch	*Fringilla coelebs*	no	63	92	66	89
Chiffchaff	*Phylloscopus collybita*	no	32	34	25	41
Coal tit	*Periparus ater*	no	6	16	12	10
Collared dove	*Streptopelia decaocto*	no	15	14	12	17
Dunnock	*Prunella modularis*	no	7	20	18	9
Goldfinch	*Carduelis carduelis*	no	244	506	375	375
Great spotted woodpecker	*Dendrocopos major*	no	14	24	23	15
Great tit	*Parus major*	no	21	26	16	31
Green woodpecker	*Picus viridis*	no	32	78	57	53
Grey heron	*Ardea cinerea*	no	3	4	1	6
Grey wagtail	*Motacilla cinerea*	no	13	0	0	13
Herring gull	*Larus argentatus*	no	27	0	0	27
Jackdaw	*Corvus monedula*	no	161	204	160	205
Jay	*Garrulus glandarius*	no	19	22	19	22
Kestrel	*Falco tinnunculus*	no	11	17	12	16
Little owl	*Athene noctua*	no	0	5	5	0
Long-tailed tit	*Aegithalos caudatus*	no	41	46	28	59
Magpie	*Pica pica*	no	81	99	83	97
Mallard	*Anas platyrhynchos*	no	4	1	1	4
Meadow pipit	*Anthus pratensis*	no	10	3	3	10

Moorhen	*Gallinula chloropus*	no	1	2	2	1
Nuthatch	*Sitta europaea*	no	25	3	1	27
Pheasant	*Phasianus colchicus*	no	102	143	123	122
Pied wagtail	*Motacilla alba*	no	1	6	1	6
Raven	*Corvus corax*	no	6	2	2	6
Red kite	*Milvus milvus*	no	2	0	0	2
Red legged partridge	*Alectoris rufa*	no	25	36	48	13
Redstart	*Phoenicurus phoenicurus*	no	0	1	0	1
Robin	*Erithacus rubecula*	no	66	74	62	78
Rook	*Corvus frugilegus*	no	25	139	149	15
Snipe	*Gallinago gallinago*	no	20	0	0	20
Sparrowhawk	*Accipiter nisus*	no	76	4	2	78
Stock dove	*Columba oenas*	no	10	2	0	12
Tawny owl	*Strix aluco*	no	1	3	3	1
Treecreeper	*Certhia familiaris*	no	3	0	3	0
Whitethroat	*Sylvia communis*	no	2	0	0	2
Wood Pigeon	*Columba palumbus*	no	217	377	333	261
Wren	*Troglodytes troglodytes*	no	46	21	17	50
Fieldfare	*Turdus pilaris*	yes	3	3	4	2
Greenfinch	*Carduelis chloris*	yes	11	35	15	31
House martin	*Delichon urbica*	yes	49	52	39	62
House sparrow	*Passer domesticus*	yes	95	42	35	102
Lapwing	*Vanellus vanellus*	yes	6	1	1	6
Linnet	*Carduelis cannabina*	yes	59	291	195	155
Merlin	*Falco columbarius*	yes	2	0	0	2
Mistle thrush	*Turdus viscivorus*	yes	6	24	14	16
Redpoll	*Cardeulis flammea*	yes	13	4	0	17
Redwing	*Turdus iliacus*	yes	8	3	3	8
Skylark	*Alauda arvensis*	yes	23	36	38	21
Song thrush	*Turdus philomelos*	yes	70	113	96	87
Starling	*Sturnus vulgaris*	yes	396	359	404	351
Swift	*Apus apus*	yes	21	19	19	21
Yellowhammer	*Emberiza citrinella*	yes	7	7	6	8

Table S4.5.2. Number of individuals of arthropods belonging to each of the listed orders recorded across either certified-organic (n=10) and non-organic (n=12) vineyards, or across Sustainable Wines of Great Britain scheme (SWGB) accredited (n=11) or not accredited (n=11) vineyards.

Order	Certified-organic	Non-organic	SWGB-accredited	non-SWGB
Acari	16	24	19	21
Araneae	1006	1149	1207	948
Archaeognatha	204	721	687	238
Chilopoda	8	40	36	12
Coleoptera	1210	835	1269	776
Collembola	78	166	172	72
Dermaptera	3	53	42	14
Diplopoda	60	92	100	52
Diptera	96	265	253	108
Hemiptera	54	0	0	54
Hymenoptera	480	1387	1143	724
Isopoda	49	105	122	32
Neuroptera	0	2	2	0
Opiliones	25	169	169	25
Orthopoda	7	9	11	5
Pseuroscorpiones	1	0	0	1
Psocoptera	0	1	1	0
Thysanoptera	5	6	2	9
Thysanura	189	211	260	140

S4.6. Model outputs

Table S4.6.1. Landscape (A, B) and local (C) scale modelled effects (and 95% confidence intervals) of landscape, habitat and management predictors on bird abundance, species richness and Shannon diversity, with reported conditional standard error (Cond. SE), t-value, p-value, and Akaike Information Criterion (AIC). nu and rho are correlation parameters that describe the spatial Matérn function that was fitted as a random effect to GLMMs to account for spatial autocorrelation of data points. Sampling season and year were added as categorical fixed effects, and an interaction term between ground vegetation cover and season was included, as vegetation cover was not independent of season. Landscape composition predictors were measured at the landscape-scale within a 2.5 km buffer around each study vineyard (n=22), and management predictors were measured at the site level. At the local scale, landscape and habitat predictors were measured within 200-meter buffer of point counts (n=44). Significant effects (when estimates with 95% CI do not span zero, and p < 0.05) are highlighted in blue.

Response	Predictors	Estimate (CI)	Cond. SE	t-value	P-value	nu	rho	AIC
(A) Birds - comparison between vineyards based on management								
Abundance (logged)	Intercept (not certified organic; not SWGB-accredited; year 2021, season budding)	3.010 (2.818; 3.199)	0.095	31.798	<0.001	0.309	0.003	1438.56
	Certified organic - yes	-0.072 (-0.279; 0.143)	0.104	-0.691	0.494			
	SWGB-accredited - yes	-0.067 (-0.253; 0.0120)	0.093	-0.723	0.473			
	Season flowering	0.175 (0.117; 0.233)	0.030	5.917	<0.001			
	Season harvest	0.585 (0.528; 0.642)	0.029	20.162				
	Year 2022	-0.029 (-0.076; 0.019)	0.024	-1.189	0.235			
Species richness	Intercept (not certified organic; not SWGB-accredited; year 2021, season budding)	9.394 (8.702; 10.104)	0.331	28.410	<0.001	0.061	0.0006	540.14
	Certified organic - yes	-0.255 (-0.957; 0.432)	0.339	-0.751	0.458			
	SWGB-accredited - yes	-0.722 (-1.404; -0.050)	0.329	-2.196	0.036			
	Season flowering	-0.047 (-0.347; 0.253	0.153	-0.307	0.018			
	Season harvest	0.344 (0.049; 0.638)	0.150	2.291				
	Year 2022	-0.436 (-0.681; -0.190)	0.125	-3.483	<0.001			
Shannon diveristy	Intercept (not certified organic; not SWGB-accredited; year 2021, season budding)	1.951 (1.834; 2.063)	0.056	34.731	<0.001	0.165	0.0004	215.31
	Certified organic - yes	0.009 (-0.111; 0.134)	0.060	0.157	0.876			
	SWGB-accredited - yes	-0.149 (-0.262; -0.029)	0.057	-2.631	0.012			
	Season flowering	0.032 (-0.003; 0.067)	0.018	1.791	<0.001			
	Season harvest	-0.043 (-0.078; -0.009)	0.018	-2.459				
	Year 2022	0.026 (-0.002; 0.055)	0.015	1.793	0.072			
(B) Bird - landscape scale models								
Abundance (logged)	Intercept (season budding, year 2021)	3.766 (1.99; 5.51)	0.875	4.305	<0.001	0.005	0.002	298.83
	Practice score	0.006 (-0.05; 0.06)	0.026	0.225	0.823			
	Ecotoxicity frequency score	0.006 (-0.005; 0.02)	0.005	1.193	0.241			
	Ecotoxicity score	0.000003 (-0.01; 0.009)	0.004	0.001	0.999			
	Ground vegetation volume	0.080 (-0.12; 0.28)	0.103	0.777	0.900			
	Season flowering	0.356 (-0.15; 0.86)	0.255	1.395	0.003			
	Season harvest	0.920 (0.40; 1.44)	0.264	3.479				
	Wood cover	0.006 (-0.02; 0.03)	0.011	0.520	0.606			
	Length of linear water features	-0.022 (-0.05; 0.009)	0.015	-1.417	0.166			
	Average field size	-0.116 (-0.32; 0.10)	0.101	-1.154	0.255			
	Year 2022	-0.031 (-0.18; 0.11)	0.073	-0.428	0.669			
	Ground vegetation volume : season flowering	-0.115 (-0.39; 0.16)	0.140	-0.822	0.447			
	Ground vegetation volume : season harvest	-0.192 (-0.50; 0.11)	0.155	-1.240				
Species Richness	Intercept (season budding, year 2021)	12.502 (6.40; 18.60)	3.096	4.038	<0.001	0.005	0.002	845.44
	Practice score	-0.030 (-0.21; 0.14)	0.089	-0.343	0.732			
	Ecotoxicity frequency score	0.002 (-0.03; 0.04)	0.017	0.118	0.906			
	Ecotoxicity score	-0.020 (-0.05; 0.01)	0.015	-1.368	0.173			
	Ground vegetation volume	0.056 (-0.87; 0.98)	0.471	0.120	0.819			
	Season flowering	-0.170 (-2.56; 2.22)	1.215	-0.140	0.467			

	Season harvest	1.340 (-1.13; 3.81)	1.251	1.071				
	Wood cover	-0.026 (-0.10; 0.05)	0.039	-0.668	0.505			
	Length of linear water features	-0.022 (-0.12; 0.08)	0.052	-0.434	0.665			
	Average field size	-0.277 (-0.96; 0.41)	0.349	-0.795	0.428			
	Year 2022	-0.364 (-1.06; 0.33)	0.354	-1.027	0.306			
	Ground vegetation volume : season flowering	0.062 (-1.25; 1.37)	0.664	0.094	0.630			
	Ground vegetation volume : season harvest	-0.589 (-2.03; 0.85)	0.732	-0.804				
Shannon (H)	Intercept (season budding, year 2021)	2.708 (1.96; 3.51)	0.378	7.172	<0.001	16.67	0.002	64.38
	Practice score	-0.002 (-0.03; 0.02)	0.011	-0.163	0.872			
	Ecotoxicity frequency score	-0.002 (-0.007; 0.003)	0.002	-0.766	0.453			
	Ecotoxicity score	-0.05 (-0.09; -0.01)	0.002	-2.662	0.019			
	Ground vegetation volume	0.106 (0.002; 0.22)	0.054	2.010	0.026			
	Season flowering	0.067 (-0.20; 0.34)	0.138	0.488	0.865			
	Season harvest	-0.002 (-0.28; 0.28)	0.142	-0.015				
	Wood cover	-0.009 (-0.02; 0.001)	0.005	-1.870	0.074			
	Length of linear water features	0.006 (-0.007; 0.02)	0.007	0.965	0.347			
	Average field size	-0.071 (-0.16; 0.02)	0.043	-1.657	0.109			
	Year 2022	0.044 (-0.04; 0.12)	0.040	1.102	0.272			
	Ground vegetation volume : season flowering	-0.037 (-0.19; 0.11)	0.075	-0.490	0.840			
	Ground vegetation volume : season harvest	-0.043 (-0.21; 0.12)	0.083	-0.520				
(C) Bird - local scale models								
Abundance (logged)	Intercept (season budding, year 2021)	2.958 (1.38; 4.51)	0.770	3.840	<0.001	0.567	0.003	341.62
	Vine cover	0.132 (-0.37; 0.63)	0.245	0.539	0.594			
	Wood cover	-0.007 (-0.02; 0.002)	0.004	-1.548	0.129			
	Linear wooded features length	-0.028 (-0.24; 0.19)	0.106	-0.266	0.792			
	Ground vegetation volume	0.131 (-0.05; 0.31)	0.089	1.473	0.390			
	Season flowering	0.400 (-0.04; 0.84)	0.220	1.823	0.001			
	Season harvest	0.754 (0.34; 1.17)	0.206	3.654				
	Year 2022	-0.028 (-0.16; 0.10)	0.064	-0.433	0.665			
	Ground vegetation volume : season flowering	-0.142 (-0.39; 0.11)	0.124	-1.141	0.484			
	Ground vegetation volume : season harvest	-0.111 (-0.36; 0.14)	0.126	-0.879				
Species Richness	Intercept (season budding, year 2021)	13.061 (7.00; 19.13)	3.081	4.240	<0.001	0.005	0.0001	1068.84
	Vine cover	0.735 (-1.11; 2.58)	0.937	0.784	0.434			
	Wood cover	-0.019 (-0.05; 0.02)	0.018	-1.108	0.269			
	Linear wooded features length	-0.616 (-1.43; 0.20)	0.415	-1.484	0.139			
	Ground vegetation volume	0.009 (-0.92; 0.94)	0.471	0.018	0.561			
	Season flowering	-0.456 (-2.84; 1.93)	1.213	-0.376	0.894			
	Season harvest	0.130 (-2.09; 2.35)	1.126	0.115				
	Year 2022	-0.617 (-1.32; 0.09)	0.361	-1.711	0.088			
	Ground vegetation volume : season flowering	0.317 (-1.03; 1.66)	0.683	0.464	0.897			
	Ground vegetation volume : season harvest	0.179 (-1.17; 1.53)	0.686	0.261				
Shannon (H)	Intercept (season budding, year 2021)	2.135 (1.34; 2.92)	0.393	5.428	<0.001	0.222	0.001	97.36
	Vine cover	-0.326 (-0.59; -0.07)	0.127	-2.559	0.018			
	Wood cover	-0.0004 (-0.006; 0.004)	0.002	-0.186	0.853			
	Linear wooded features length	-0.038 (-0.15; 0.07)	0.054	-0.714	0.479			
	Ground vegetation volume	0.095 (0.01; 0.20)	0.051	1.866	0.018			
	Season flowering	-0.008 (-0.26; 0.24)	0.128	-0.066	0.983			
	Season harvest	0.016 (-0.22; 0.25)	0.120	0.136				
	Year 2022	0.018 (-0.06; 0.09)	0.038	0.488	0.626			
	Ground vegetation volume * Season flowering	0.0002 (-0.14; 0.14)	0.072	0.003	0.726			
	Ground vegetation volume * Season harvest	-0.052 (-0.20; 0.09)	0.073	-0.709				

Table S4.6.2. Landscape (A, B, C, E) and local (D) scale modelled effects (and 95% confidence intervals) of landscape, habitat and management predictors on arthropod presence, abundance and Shannon diversity, with reported conditional standard error (Cond. SE), t-value, p-value, and Akaike Information Criterion (AIC). nu and rho are correlation parameters that describe spatial Matérn function that was fitted as a random effect to GLMMs to account for spatial autocorrelation of data points. Sampling season and year were added as categorical fixed effects, and an interaction term between ground vegetation cover and season was included, as vegetation cover was not independent of season. Landscape composition predictors were measured at the landscape-scale within a 2.5 km buffer around each study vineyard (n=22), and management predictors were measured at the site level. At the local scale, landscape and habitat predictors were measured within 100-meter buffer of transects (n=79). Significant effects (when estimates with 95% CI do not span zero, and p < 0.05) are highlighted in blue.

Response	Predictors	Estimate (CI)	Cond. SE	t-value	P-value	nu	rho	AIC
(D) Arthropod - comparison between vineyards based on management								
Abundance	Intercept (not certified organic; not SWGB-accredited; year 2021, season budding)	2.033 (1.765; 2.347)	0.133	15.327	<0.001	0.036	0.00003	2958.95
	Certified organic - yes	0.283 (0.035; 0.542)	0.120	2.354	0.024			
	SWGB-accredited - yes	-0.041 (-0.312; 0.218)	0.129	-0.315	0.755			
	Season flowering	-0.192 (-0.325; -0.058)	0.068	-2.300	<0.001			
	Season harvest	-0.495 (-0.629; -0.361)	0.068	-7.302				
	Year 2022	-0.105 (-0.207; -0.002)	0.052	-2.000	0.046			
Shannon diveristy	Intercept (not certified organic; not SWGB-accredited; year 2021, season budding)	1.138 (1.02; 1.26)	0.059	19.244	<0.001	0.073	0.0006	796.06
	Certified organic - yes	0.066 (-0.044; 0.175)	0.053	1.251	0.218			
	SWGB-accredited - yes	-0.046 (-0.164; 0.071)	0.058	-0.789	0.438			
	Season flowering	-0.059 (-0.124; 0.006)	0.033	-1.793	0.004			
	Season harvest	-0.109 (-0.175; -0.043)	0.033	-3.280				
	Year 2022	0.071 (0.020; 0.122)	0.026	2.738	0.006			
(E) Arthropod - landscape scale hurdle model								
Presence / absence	Intercept (season budding, year 2021)	-1.674 (-3.24; -0.10)	0.698	-2.398	0.027	16.667	0.00002	1776.14
	Practice score	0.131 (0.08; 0.19)	0.024	5.558	<0.001			
	Ecotoxicity frequency score	0.004 (-0.01; 0.02)	0.005	0.964	0.401			
	Ecotoxicity score	0.007 (-0.01; 0.01)	0.004	1.749	0.379			
	Ground vegetation volume	0.141 (0.09; 0.19)	0.025	5.523	<0.001			
	Season flowering	0.939 (0.58; 1.30)	0.177	5.296	<0.001			
	Season harvest	1.504 (1.09; 1.92)	0.209	7.189				
	Wood cover	0.025 (-0.003; 0.05)	0.010	1.905	0.098			
	Length of linear water features	0.003 (-0.05; 0.06)	0.014	0.218	0.05			
	Average field size	-0.038 (-0.004; 0.004)	0.057	-0.660	0.814			
	Year 2022	-0.436 (-0.59; -0.29)	0.077	-5.697	<0.001			
	Distance	-0.05 (-0.08; -0.02)	0.001	-3.311	<0.001			
	Ground vegetation volume : season flowering	0.012 (-0.05; 0.02)	0.026	1.876	0.064			
	Ground vegetation volume : season harvest	0.020 (-0.03; 0.1)	0.033	1.654				
Abundance	Intercept (season budding, year 2021)	1.799 (-0.85; 5.09)	1.009	1.783	0.075	16.667	0.0002	5418.54
	Practice score	0.201 (0.09; 0.31)	0.031	2.439	0.015			
	Ecotoxicity frequency score	0.001 (-0.01; 0.01)	0.005	0.274	0.784			
	Ecotoxicity score	-0.10 (-0.2; -0.01)	0.005	-2.026	0.043			
	Ground vegetation volume	0.213 (0.01; 0.42)	0.100	2.127	0.033			
	Season flowering	0.077 (-0.38; 0.59)	0.231	0.335	0.737			
	Season harvest	-0.122 (-0.73; 0.39)	0.253	-0.481				
	Wood cover	0.016 (-0.02; 0.05)	0.010	1.531	0.630			
	Length of linear water features	0.0001 (-0.06; 0.06)	0.023	0.006	0.126			
	Average field size	0.017 (-0.51; 0.99)	0.107	0.162	0.995			
	Year 2022	-0.150 (-0.29; -0.01)	0.069	-2.164	0.030			
	Distance	0.0004 (-0.0001; 0.003)	0.001	0.326	0.871			
	Ground vegetation volume : season flowering	-0.053 (-0.34; 0.20)	0.126	-0.421	0.745			

	Ground vegetation volume : season harvest	-0.198 (-0.49; 0.13)	0.145	-1.366				
Shannon (H)	Intercept (season budding, year 2021)	1.149 (0.59; 1.71)	0.281	4.094	<0.001	0.005	0.005	641.98
	Practice score	0.008 (-0.007; 0.02)	0.008	1.055	0.295			
	Ecotoxicity frequency score	-0.06 (-0.03; -0.09)	0.001	-3.987	<0.001			
	Ecotoxicity score	-0.03 (-0.05; -0.005)	0.001	-2.415	0.019			
	Ground vegetation volume	0.113 (0.03; 0.20)	0.043	2.610	<0.001			
	Season flowering	-0.143 (-0.34; 0.06)	0.101	-1.413	0.250			
	Season harvest	-0.171 (-0.40; 0.06)	0.116	-1.477				
	Wood cover	0.005 (-0.002; 0.01)	0.003	1.356	0.179			
	Length of linear water features	0.002 (-0.008; 0.012)	0.005	0.475	0.636			
	Average field size	-0.053 (-0.002; 0.008)	0.031	-1.721	0.089			
	Year 2022	0.058 (-0.001; 0.12)	0.030	1.946	0.052			
	Distance	-0.0002 (-0.001; 0.0008)	0.001	-0.441	0.660			
	Ground vegetation volume : season flowering	0.020 (-0.09; 0.13)	0.055	0.372	0.926			
	Ground vegetation volume : season harvest	0.0197 (-0.11; 0.15)	0.066	0.298				
(F) Arthropod - truncated local scale model								
Abundance	Intercept (season budding, year 2021, boundary hedgerow)	2.855 (0.76; 4.96)	1.049	2.723	0.006	0.089	0.0007	600.09
	Ground vegetation volume	0.229 (0.05; 0.40)	0.089	4.717	<0.001			
	Season flowering	0.005 (-0.41; 0.42)	0.211	0.026	0.980			
	Season harvest	-0.169 (-0.62; 0.28)	0.227	-0.742				
	Boundary open	-0.04 (-0.32; 0.23)	0.135	-0.316	0.458			
	Boundary wood	0.012 (-0.20; 0.23)	0.108	0.107				
	Distance	-0.0002 (-0.002; 0.002)	0.001	-0.234	0.752			
	Year 2022	-0.169 (-0.25; -0.09)	0.063	-4.213	0.011			
	Vine cover	-0.086 (-0.27; 0.10)	0.092	-0.935	0.815			
	Ground vegetation volume : season flowering	-0.051 (-0.28; 0.18)	0.115	-0.441	0.055			
	Ground vegetation volume : season harvest	-0.175 (-0.43; 0.08)	0.130	-1.342				
Shannon (H)	Intercept (season budding, year 2021, boundary hedgerow)	0.928 (0.18; 1.68)	0.372	2.495	<0.001	0.013	0.0008	721.96
	Ground vegetation volume	0.158 (0.11; 0.21)	0.040	6.067	<0.001			
	Season flowering	-0.179 (-0.36; 0.01)	0.095	-1.887	0.146			
	Season harvest	-0.143 (-0.35; 0.06)	0.104	-1.382				
	Boundary open	-0.030 (-0.13; 0.07)	0.047	-0.639	0.809			
	Boundary wood	-0.015 (-0.09; 0.06)	0.039	-0.375				
	Distance	-0.0003 (-0.001; 0.001)	0.001	-0.527	0.599			
	Year 2022	0.054 (-0.002; 0.11)	0.029	1.886	0.060			
	Vine cover	0.011 (-0.05; 0.08)	0.032	0.337	0.738			
	Ground vegetation volume : season flowering	0.060 (-0.04; 0.16)	0.052	1.152	0.500			
	Ground vegetation volume : season harvest	0.020 (-0.10; 0.14)	0.060	0.341				
(G) Arthropod - truncated landscape scale model - with full dataset (outlier retained)								
Abundance	Intercept (season budding, year 2021)	3.155 (0.981: 4.995)	0.904	3.491	<0.001	16.667	0.0006	5452.89
	Practice score	0.061 (0.001, 0.103)	0.030	2.058	0.040			
	Ecotoxicity frequency score	0.006 (-0.006; 0.017)	0.005	1.031	0.303			
	Ecotoxicity score	-0.001 (-0.013; 0.009)	0.005	-0.206	0.837			
	Ground vegetation volume	0.235 (0.037; 0.432)	0.099	2.371	0.018			
	Season flowering	0.099 (-0.350; 0.548)	0.228	0.434	0.664			
	Season harvest	-0.216 (-0.733; 0.299)	0.260	-0.829				
	Wood cover	0.021(-0.005; 0.045)	0.012	1.748	0.407			
	Length of linear water features	-0.009 (-0.045; 0.029)	0.018	-0.517	0.080			
	Average field size	-0.172 (-0.362; 0.018)	0.103	-1.664	0.605			
	Year 2022	-0.140 (-0.283; 0.001)	0.067	-2.073	0.051			
	Distance	0.0001 (-0.002; 0.002)	0.001	0.149	0.380			
	Ground vegetation volume : season flowering	-0.097 (-0.343; 0.148)	0.125	-0.778	0.882			
	Ground vegetation volume : season harvest	-0.167 (-0.460; 0.126)	0.148	-1.128				

Table S4.6.3. Modelled effects (and 95% confidence intervals) of ground vegetation management practices and field size on ground vegetation cover across 22 study vineyards, with reported estimates and 95% confidence intervals (CI), standard error, t-value, p-value, and Akaike Information Criterion (AIC). Significant effects (when estimates with 95% CI do not span zero, and $p < 0.05$) are highlighted in blue.

Predictors	Estimate (CI)	Std. Error	t-value	P-value	AIC
(H) Ground vegetation cover					
Intercept (no herbicide; no cover crops of wildflowers)	-0.394 (-0.74; -0.04)	0.176	-2.242	0.041	95.83
Mowing frequency	0.007 (-0.02; 0.03)	0.012	0.559	0.585	
Cultivation frequency	-0.019 (-0.04; 0.01)	0.013	-1.457	0.166	
Average field size	-0.120 (0.03; 0.20)	0.043	-2.784	0.014	
Herbicide use (binary)	-0.077 (0.02; 0.13)	0.028	-2.760	0.015	
Sowing cover crops or wildflowers (binary)	0.026 (-0.04; 0.09)	0.034	0.763	0.457	

S4.7. Comparison of management variables between vineyards varying in the overall management regime

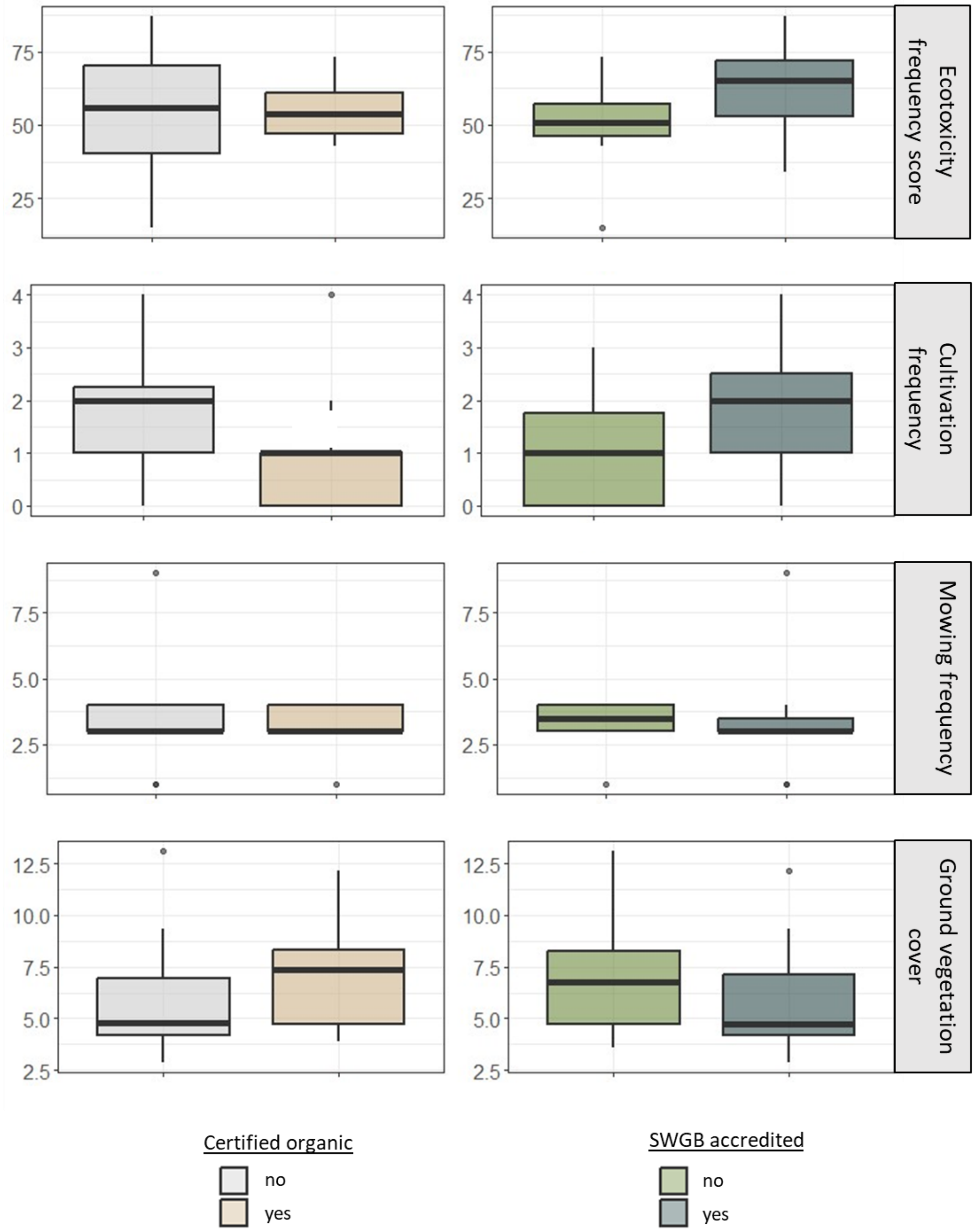


Figure S4.7. Comparison of vineyard management predictors between vineyards that were certified organic (n=10/22) and non-certified organic, as well as those that were Sustainable Wines of Great Britain (SWGB) accredited (n=11/22) and those without the accreditation. Ecotoxicity frequency score is derived from agrochemical use data (see S4.3. for more information), cultivating and mowing frequency are given as counts per year, and ground vegetation cover is a metric we computed based on ground vegetation height and proportion ground cover (see 4.2.3. for details).

Chapter 5: The impact of bird communities on yield can be mitigated by vineyard management and configuration: lessons from English vineyards.

© Natalia Zielonka: Eurasian starlings *Sturnus vulgaris* perching over a vineyards in Kent.

Natalia B. Zielonka[a], Jack D. Shutt[b], Simon J. Butler[a*] & Lynn V. Dicks[a,b*]

[a] School of Biological Sciences, University of East Anglia, Norwich, UK, NR4 7TJ
[b] Department of Zoology, University of Cambridge, UK, CB2 3EJ

* *joint last authors*

Abstract

Birds are ever-present across agricultural systems and contribute an array of services, such as biological pest control, and disservices, such as crop damage. The provision of both is affected by the on-farm management and characteristics of the surrounding landscapes, and within one system the net effect of birds can result in a gain or loss for production. Grapevines are an important global crop, and in the UK, the viticultural industry is the fastest growing agricultural sector, where birds are seen as common grape pests. Here, through grape damage assessments, experimental exclusion of birds and insects, and by using the relative abundances of service- and disservice- providing bird species as proxies for functionality, we assess the net effect of birds on grape production. Overall, birds contributed the most to grape damage (7.9%), which decreased significantly with distance away from field edges, was significantly higher by woodland (+42%) compared to open boundaries and was significantly lower in 2022 (-33%) than 2021. Damage by insects was low (constituting 0.83%) and it did not vary spatially or temporally. At harvest, 62% of recorded birds were considered grape-eaters and seven of the 16 grape-eating species are national conservation priorities. The abundance of grape-eaters was significantly and positively related to grape damage, but this was only associated with a significantly lower yield in vineyards with a high field edge density. Interestingly, grape yield, in tonnes per hectare, was significantly higher in 2022 (+22%) than in 2021, and it was significantly lower in certified-organic (-36%) than non-organic vineyards, which we hypothesise could be due to reduced vine vigour in certified-organic vineyards and higher average field edge density increasing the impacts of frugivory. Management of bird damage in vineyards needs to be handled sensitively, and our findings lend themselves to management and policy recommendations: (i) bird management should be targeted at fields edges by woodlands and in small fields, (ii) retaining wider grassland strips that separate vine fields from boundary habitats could both reduce damage and boost biodiversity, and (iii) the costs arising from bird activity could be compensated for by industry sustainability schemes, or offset by higher wine retail prices.

Acknowledgements

We sincerely thank our study vineyards' managers and employees for access to field sites, in-field logistics, for providing management information, and their support and interest in our research. We thank WineGB and SWGB, and Chris Foss in particular, for their help in setting up this project and for supporting our research. We thank Katarzyna Zielonka for her assistance in fieldwork. This work and Natalia Zielonka were funded by the UKRI Biotechnology and Biological Sciences Research Council Norwich Research Park Biosciences Doctoral Training Partnership [Grant number BB/M011216/1].

5.1. Introduction

Biodiversity within agricultural landscapes brings both benefits and costs to production (Zhang *et al.*, 2007), and the relationship between conservation and farming is a complicated one. Agriculture is a key driver of biodiversity decline worldwide (Jaureguiberry *et al.*, 2022; van Klink *et al.*, 2020), yet it is nested within nature, relying on ecosystem services, such as pollination and biological pest control (Díaz *et al.*, 2018). However, intensive agricultural practices, such as agrochemical use, accelerate biodiversity declines (Rigal *et al.*, 2023), and through this, accelerate the loss of nature's services (Hendershot *et al.*, 2020; Kremen & Merenlender, 2018). Ecological intensification, which aims to harness ecosystem services that enhance production (Bommarco *et al.*, 2013; Kleijn *et al.*, 2019) promises to reduce the impacts of high yielding food production on biodiversity, and is promoted in policy, for example as a target in the new Global Biodiversity Framework's: "*through a substantial increase of the application of biodiversity friendly practices, such as sustainable intensification*, (…) *conserving and restoring biodiversity and maintaining nature's contributions to people, including ecosystem functions and services.*" (Keping, 2023). However, biodiversity also contributes ecosystem disservices, such as crop damage, which reduce agricultural productivity, and this generates an important question: on balance, how much biodiversity is good for production, when both services and disservices are taken into account?

Birds are ever-present across agricultural systems and contribute an array of services and disservices, yet they are also declining due to land-use change and agricultural intensification (Bowler *et al.*, 2019; Rigal *et al.*, 2023). The awareness of birds' role in crop damage is high, particularly among farmers, likely because disservices often result directly from bird activity (Peisley *et al.*, 2015), and direct crop damage through frugivory has been well-studied (Lindell *et al.*, 2012; Mangan *et al.*, 2017; Peisley *et al.*, 2017). Birds' contributions as biological control agents in supressing both insect and vertebrate pests have been well documented (Díaz-Siefer *et al.*, 2022), including in fruit orchards and vineyards (Barbaro *et al.*, 2017; Peisley *et al.*, 2016), though they remain frequently overlooked (Garcia *et al.*, 2020). Taken together, this means that there are trade-offs between bird costs and benefits. For example, through experimental exclusion, Peisley *et al.* (2016) demonstrated this in Australian apple orchards, where birds contributed both costs and benefits, yet their contributions to reducing insect damage through pest control were 3-fold greater than of direct bird damage, and therefore, their presence led to an overall 11% increase in yield. Studies that quantify both services and disservices remain rare (Peisley *et al.*, 2015) but are necessary to inform evidence-based management, as one action to exclude bird species to minimise crop damage could result in the loss of another service, such as pest control, and increase the reliance on environmentally harmful agrochemicals (Bennett *et al.*, 2009).

Studies have demonstrated that bird-mediated ecosystem services and disservices are affected by both on-farm management and characteristics of the surrounding landscape (Pejchar *et al.*, 2018; Zhang *et al.*, 2007), meaning that the net impact of birds varies spatially. Lower levels of natural pest control have been well documented in simple landscapes and have largely been attributed to a reduction in avian species richness (Dainese *et al.*, 2019; Rusch *et al.*, 2016). Globally, pest control by birds has been shown to significantly increase yield on conventional but not organic farms, likely because organic farms had higher abundances of non-avian natural enemies, such as predatory arthropods, already present (Díaz-Siefer *et al.*, 2022). Higher levels of frugivory by birds have also been noted in simple landscapes, likely due to the lower availability of alternative food resources (Gonthier *et al.*, 2019; Smith *et al.*, 2022). These dynamics happen simultaneously within a single agricultural system and trade-off, resulting in net gain or loss for production. Landscape complexity and biodiversity-friendly practices have been shown to increase community evenness and thus, temporally stabilise ecosystem provision, making their impact predictable and increasing their value to production (Barbaro *et al.*, 2021; Linden *et al.*, 2019; Smith *et al.*, 2022). This has been demonstrated across Californian strawberry farms, where the balance between provision of ecosystem services and disservices shifted in response to landscape complexity; in simple landscapes birds inflicted more direct fruit damage alongside providing pest control, whilst in complex landscapes, birds were more likely to disrupt pest control through intraguild predation (Olimpi *et al.*, 2020). When taken together, the overall net effect of birds was slightly negative in all cases, but disservices were lowered by landscape complexity (Olimpi *et al.* 2020).

Grapevines are an important global crop, with over 7 million hectares of land dedicated to their production, which accounts for about 5% of the global cover by perennial crops (Ritchie & Roser, 2013; Venkitasamy *et al.*, 2019). Birds contribute to an array of ecosystem services, such as pest control, and disservices, namely through frugivory, across vineyards (Winkler *et al.*, 2017), but their net outcome seems highly contextual as a recent global synthesis showed no significant effect of bird exclusion on viticulture (Díaz-Siefer *et al.*, 2022). This is probably because losses from bird-mediated disservices offset any gains from services, when considered across studies at large scales. Across vineyards, rates of frugivory by birds have been shown to be as high as 80% (Fukuda *et al.*, 2008; Kross *et al.*, 2012), and to vary spatially with more grape damage occurring around vineyard edges that neighbour semi-natural habitats (Patyal & Rana, 2005; Peisley *et al.*, 2017; Somers & Morris, 2002). The relationship between semi-natural habitats cover and pest control by birds is also complex as whilst semi-natural habitats were shown to enhance the service in more heterogeneous landscapes, the opposite effect was shown in vineyard-dominated landscapes (Barbaro *et al.*, 2017).

Compared to other regions, the viticultural industry in the UK is small but has become the fastest growing agricultural sector, which is attributed to increasing summer temperatures making the climate increasingly viable (Nesbitt *et al.*, 2019). As the industry is relatively new, it lacks an assessment of the contributions of biodiversity to ecosystem services and disservices, though a recent survey conducted across British vineyards found 35% respondents to consider wasps and 20% of respondents to consider birds as the main pest group (Griffiths-Lee *et al.*, 2022). By working across English vineyards spanning gradients of landscape complexity and management practices, our first objective was to assess the net effect of birds on grape production. Secondly, we wished to address the current literature gap in European-focussed studies that measure the net-effects of birds (Peisley *et al.*, 2015), whilst considering the interplay between bird communities, landscape complexity, on-farm management, and yield within a single study. Through grape damage assessments, experimental exclusion of birds and insects, and by using the relative abundances of service- and disservice- providing bird species as proxies for functionality, our aims were to: (1) quantify the levels of grape damage caused by birds and insects, (2) assess the spatial variation in grape damage, relating it to landscape complexity, vineyard configuration and management practices, (3) understand the relationship between vineyard bird communities and the levels of bird and insect damage, (4) measure the yield impacts of grape damage by birds and insects, and (5) consider the effects of farm management and vineyard configuration on yield.

5.2. Methods and materials

5.2.1. Study sites

This study took place across 16 English vineyards, spanning UK's key wine-growing regions (Chapter 3). All fieldwork was repeated in 2021 and in 2022 and aligned with the key stages of the vine lifecycle: 'budding' (early to mid-April), 'flowering' (late June-mid-July), and at 'harvest' (September and October).

Landscape and management predictors

Sites were chosen to represent the broader English viticultural industry and they span landscape complexity and management gradients, with six being certified-organic, and nine being accredited through the Sustainable Wines of Great Britain (SWGB) accreditation scheme (including one site being accredited through both, and three sites through neither; see Chapter 3 and 4 for details). The average study vineyard was 16.23 ha ± 4.98 (SE, range 1.2 – 82.1), which is larger than the UK average of 6.85 ± 0.6 ha, as small vineyards dominate the British industry (median size: 2.8 ha, n=460 after exclusion of vineyards <1 ha; Skelton, = 2022). We quantified the variation in field configuration across our sites by calculating field edge density (m / ha), which was the total length of vine field edges (m) divided by the hectares of planted vines per site (mean 314 m / ha, range 193 - 439). All of our study vineyards grew at least two of the four most planted grape varieties in Great Britain (Chardonnay, Pinot Noir, Pinot Meunier and Bacchus; WineGB, 2023), and were at least three years old in 2021, thus were expecting to harvest grapes.

We quantified the cover by semi-natural habitats within a 2.5 km landscape buffer around a central point of each site using the CEH Land cover 2021 map (Marston *et al.*, 2022) in QGIS (3.30.00). We summed the cover of woodland (combining coniferous woodlands, which made up ~8% of total woodland cover, with deciduous) and semi-natural grasslands to give us the cover of semi-natural habitats (*SNH-cover)* around our sites. The average SNH-cover in the landscape buffers surrounding our sites was 16.3% (range 1% - 37%). Three types of boundary habitat that varied in structural complexity surrounded vine fields: open boundaries, which lacked any habitat features, hedgerows and woodlands.

For each study field and survey season, we computed a *ground vegetation cover* metric, which summarised ground vegetation cover and height (see Chapter 4 for details). For each vineyard, we obtained management information through a management survey completed by site managers (see Chapter 4), where we collected information on chemical inputs, vineyard management practices and yield, in tonnes per hectare, at the vineyard scale across our study sites. We summarised agrochemical inputs in terms of environmental toxicity (henceforth '*ecotoxicity*') by obtaining environmental ecotoxicity information for individual active ingredients from the Pesticide and Bio-pesticide Properties Databases (Lewis *et al.*, 2016; see S4.3 for details). We summed these across all active ingredients used in each vineyard to derive an overall '*ecotoxicity score*', and then we multiplied each active ingredient's *ecotoxicity score* by its number of annual applications and summed these values to calculate an '*ecotoxicity frequency score*'. We rated vineyard management practices in terms of potential benefits to or detrimental impacts on biodiversity by translating evidence assessment categories from the Conservation Evidence database (ConservationEvidence.com, 2023) into a score, and then we summed the scores for all vineyard management practices employed to calculate a '*practice score*' for each study site (see S4.3. for details). These scores were based on management across the two study years, whilst yield data were available separately for each study year.

5.2.2. Grape damage

Grape damage by birds and insects was quantified in two ways: (i) through grape damage surveys, and (ii) an exclusion experiment. To assess whether grape damage varied spatially, surveys were performed along transects that followed vine rows and ran parallel with the vine rows and away from field boundaries (Figure 5.1). Each survey field had two transects, one on the edge of the field, exposed to the boundary habitat, and one 30-50 metresinto the vine field (Figure 5.1). Survey fields (n=28) were surrounded by one of the three boundary habitats (open, hedgerow or woodland). Grape damage assessments were performed across six grape varieties, which included the top four most planted varieties that make up 77% of all plantings in England and Wales (WineGB, 2023). These were evenly split between white (51.4%) and red (48.6%) bunches.

Grape damage was assessed by the same observer in both years and followed Somers & Morris (2002), where we estimated the proportion of the whole bunch that was damaged by birds and insects. We never assessed any bunches that were >50% infected by fungal infections as that would make assessments of damage by birds or insects unreliable. Damage by birds took two forms and was characterised by missing berries (pluck damage usually caused by larger birds, such as Pheasants *Phasianus colchicus*), and secondly peck damage, which consisted of intact berry skins with some or all pulp and seeds removed (Somers & Morris, 2002, Figure 5.2a). Damage by insects was characterised by small piercings in the berry skin with the juice and pulp sucked out but with the seeds still present (Figure 5.2a). In some cases, it was difficult to reliably determine whether a small bird or an insect initiated the damage as some insects, such as wasps, are known to frequently feed on already damaged berries, removing more pulp. In these cases, it was assumed that berries with seeds still present were damaged by insects.

Grape damage assessments

Grape damage surveys were performed across 56 transects (average 3.38 transects per site, range 2-6) across the 28 fields (with each field being surrounded by one boundary habitat: open n=7, hedgerows n=11 and woodland n=10). Transects varied in length depending on the field size, but all were between 60-100 m, and grape damage was assessed on three bunches from one vine plant every 10 m, starting at 0 m. The assessed bunches were about one metre above the ground, which was the typical trellis height at which vine shoots across our sites were secured. In total, 3,018 bunches were assessed across the two years.

Exclusion experiment

The exclusion experiment included two treatments, *bird-only* and *bird+insect*, as well as a control (Figure 5.2b), and we randomly assigned each of these to one of three bunches on the same one vine plant (n=141 vine plants) at one metre above the ground. Following Nereu *et al.* 2018, we used green, plastic mesh (mesh size 8 mm) to make the exclusion bags with the bottom closed off with cable ties, and the top open to slide over the experimental bunch and secure to the vine plant. For the *bird + insect* treatment, we additionally fitted an insect mesh netting bag (mesh size 1.35 mm) over the green netting cage (Figure 5.2b). The exclusion bags were 40-45 cm in length and 15-20 cm in diameter, which was larger than the expected size of bunches, which ensured the bags did not touch the grapes.

The exclusion experiment was performed across 47 transects (average 3.13 per site, range 2-5; 12 by open boundaries, 19 by hedgerows and 12 by woodland), with the experiment being repeated in 2021 (n=44 transects) and 2022 (n=46 transects). We had up to two exclusion transects in one field, which were at least 50 m apart, and one transect in each field aligned with the 'grape assessment' survey transect that was away from the field edge (Figure 5.1). Along each transect, the experimental treatments were deployed at 0, 30 and 60 m along each transect, totalling 9 experimental bunches per transect. The same vine plants were used for the experiment across the two years.

The experimental bags were deployed at fruit set (July) and the experiment continued until harvest, when the exclusion bags were removed. During the exclusion experiment, all vineyard activities, including spraying, continued as normal. At harvest, the experimental bunches were assessed for bird and insect damage (following the protocol described in 5.2.2). Across the two years, 4 exclusion bags were damaged by farm machinery, and 16 bunches were completely diseased, preventing accurate assessment of damage, and these were excluded. In total, this resulted in 789 experimental bunches used in analyses.

5.2.3. Bird communities

In each sampling field, bird communities were assessed with 10-minute point counts three times each year (at budding, flowering and harvest), which totalled 168 surveys. Bird surveys at harvest were always performed on the same day as grape damage assessments. Point count surveys were conducted between 05:00 – 09:00 and within 3 hours of sunrise, which varied between sampling seasons. Surveys only took place on dry and still days (Bibby *et al.*, 2000), and were performed by the same observer (NBZ).

We characterised all recorded bird species by their diet using the AVONET (Tobias *et al.*, 2022) and SAviTraits 1.0 (Murphy *et al.*, 2023) databases. First, we used the AVONET database to assign each species to their main dietary group: carnivore, invertivore, vertivore, herbivore, granivore or omnivore. Due to the overlap between some of these groups, we grouped carnivores and vertivores into one category called 'carnivores', and we grouped herbivores and granivores into 'herbivores'. Secondly, we used the SAviTraits database to capture seasonal variation in species' diets and assigned species to season-specific dietary groups based on their predominant food type (see Supplementary Materials S5.1). Additionally, we identified species as 'grape-eaters' if they were observed to feed on ripened grapes by us during fieldwork, or by the vineyard managers, or if they have been previously reported in literature to feed on grapes (e.g. Lamelas-López & Marco, 2021). These species were added to an additional '*grape-eater*' group on top of their main dietary group. For each survey in each sampling field, we calculated the total bird abundance, the abundance of birds belonging to each of the four dietary groups (omnivores, carnivores, invertivores, and herbivores), and the abundance of '*grape-eaters*'.

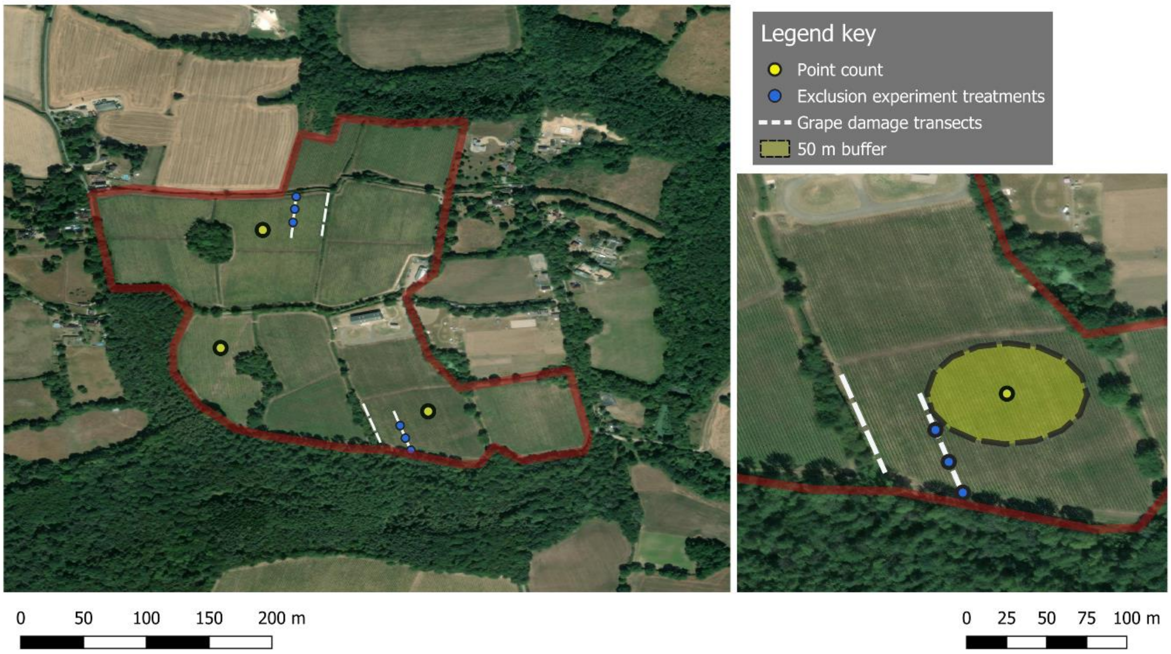
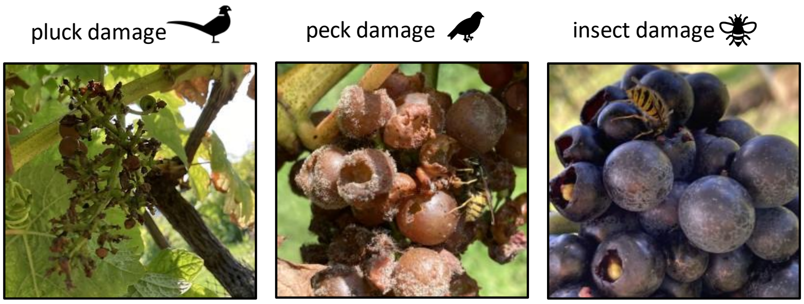


Figure 5.1. Map of an example study site showing the sampling design across a whole vineyard, and within one survey field, with the transects (white dashed lines) where grape damage surveys and exclusion experiment (blue dots) took place, as well as showing location of a bird point count survey (yellow dots) with a 50 m buffer where birds were recorded. In total, we conducted sampling across 28 transects in 16 vineyards.



(a) grape damage

(b) exclusion experiment treatments

Figure 5.2. Photos showing examples of bird (pluck and peck) and insect damage to grape bunches **(a)**, including visible fungal disease damage in the 'peck damage' example. In **(b),** the three experimental exclusion treatments are shown, including controls with no exclusion, *bird-only* exclusion bags which allowed insects to access the bunches, and *bird + insect* exclusion bags that prevented both birds and insects from accessing the bunches.

5.2.4. Statistical analyses

All analyses were conducted in R (version 4.3.0), and general(ised) linear mixed models (GLMMs) were fitted using the *glmmTMB* package (Brooks *et al.*, 2017). We proceeded with full models, accepting predictor significance if p-value < 0.05. We inspected the distribution of residuals, dispersion and checked for influential points using the *DHARMa* package (Hartig, 2022). All response and predictor variables, model structure, error terms and link functions are summarised in Supplementary Materials S5.2.

Spatial and temporal variation in grape damage by birds and insects

To evaluate the effects of birds and insects on grape damage, we modelled grape damage per bunch by birds or insects from grape assessment surveys, and then from the experimental exclusion treatments as response variables in GLMMs. First, we modelled the proportion of bird and insect damage per grape bunch, in separate models, specifying binomial error distribution. We included the fixed effects of distance from the field edge, coding all observations from transects along the edge of fields as 0 metres. We then modelled the combined damage by birds and insects from the exclusion experiment bunches, fitting a beta-binomial error distribution model, which accounted for overdispersion, of the number of individual grapes on a bunch that were predated (damaged) and non-predated (not-damaged), which accounted for the differences in bunch size. We included the fixed effects of experimental exclusion treatment, boundary type, distance from the field edge, year and grape variety. All models included nested random effects to account for the structure of data collection and more similar growing conditions, thus for grape assessment models we nested Field ID within vineyard, and for the exclusion experiment model, we nested Transect ID within Vineyard. The use of the same vine plant across the study years was accounted for by the fixed effects of experimental exclusion treatment and distance, combined with the random effects.

Relationship between grape damage and bird communities

To understand the drivers of the abundance of bird species that most likely contribute to ecosystem services or disservices in vineyards, we modelled the abundance of grape-eating, and invertebrate-eating (combining invertivore and omnivore abundance) species at harvest as response variables in GLMMs. We normalised the response variables with a log-transformation and fitted models with a Gaussian error distribution to the fixed effects of *ecotoxicity, ecotoxicity frequency* and *practice scores*, *ground vegetation cover* at harvest, SNH-cover and year. Vineyard was included as a random effect.

To evaluate whether damage to grapes by birds and insects was related to bird community composition, we evaluated bird damage in relation to the total bird abundance and the abundance of grape-eating species at harvest, and insect damage in relation to the total bird abundance and the abundance of invertebrate-eating species. Proportions of bunches damaged by birds, or insects, were averaged per field and per year and used as the response variables, and thus, we specified binomial error distribution. Each model included either the abundance of all birds, grape-eating or invertebrate-eating species in that field and year, and the fixed effect of year as predictors. Models also included a random effect of Field ID nested in Vineyard.

Relationship between grape damage, bird communities, yield and vineyard management

To identify the drivers of grape yield, we modelled the response variable of yield by fitting Gaussian error distribution GLMMs. Given that damage by birds was significantly higher at field edges and was positively related to the abundance of grape-eating species (see Results), we modelled yield in response to the fixed effects of grape-eating bird species abundance, field edge density and the interaction between these two predictors, as well as year. All numeric variables in the model were mean-centered to enable better model convergence (Schielzeth, 2010). To understand how yield varied across vineyards based on their management, we fitted yield as a response variable firstly in models with the fixed effects of certified-organic and SWGB-accreditation statuses, and secondly in relation to *ecotoxicity, ecotoxicity frequency* and *practice scores*, and average *ground vegetation cover* per vineyard. All models included the fixed effect of year, and vineyard was fitted as a random effect.

Economic impact of bird damage at a vineyard scale

To assess the extent of bird damage at a vineyard scale and its impact on yield and revenue, we paired the results from the bird grape damage models with yield data obtained through our management surveys. We did not consider insect damage as it was minimal. Based on the average field sizes across our study sites, we simulated three vine fields that varied in size: (i) smallest field size of 0.84 ha, (ii) median-sized field of 2 ha, and (iii) largest field size of 7 ha. We used model estimates with reference levels set to woodland boundary, red grapes and 2021, to predict damage for every 1 m^2 of the simulated fields by predicting the proportion of grape bunch damaged by birds (Figure 5.3.)

$$\textit{Proportion grape bunch damaged by birds} = \textit{Model predicted damage at 0m} - (\textit{0.033\% x distance to the nearest field edge}) = \textit{18\%} - (\textit{0.033\% x 10 m}) = \textit{17.67\%}$$

Figure 5.3. Example calculation of predicting grape damage at 10 m away from the field edge, using the model predicted estimate of the decrease in grape damage with distance (Supplementary Materials S5.3), relative to the predicted damage at 0 m (field edge, 18%). Reference levels used in predictions were set to woodland boundary, red grapes and 2021.

Then, we averaged the predicted damage by birds for each simulated field and used the average yield from across our study sites to show the *relative* yield losses in tonnes per hectare in each field size. The price for a tonne of grapes is around £2,000 (*Wine and Grape Trading UK*, 2023), and we used this to estimate *relative* loss of revenue per hectare in each of our simulated fields.

5.3. Results

5.3.1. Spatial and temporal variation in grape damage by birds and insects

Grape assessments

Damage by birds or insects was detected on 40.4% of surveyed bunches, but the mean proportion of damage was low, and on average, 7.9% (± 0.27 SE) of each bunch was damaged by birds, 0.83% (± 0.07) by insects, and 1.85% (± 0.11) by fungal diseases. Average damage by birds (2021: 9.2%, 2022: 6.2%), insects (2021: 0.8%, 2022: 0.78%) and disease (2021: 2.2%, 2022: 1.5%) was higher in 2021 than in 2022. Grape damage by birds decreased significantly with distance away from field edges (slope: -0.033, p-value < 0.001, Figure 5.4a), and it was significantly higher by woodland (slope: 0.870, p-value $= 0.030$) compared to open boundaries (Figure 5.4b), and it was significantly lower in 2022 than 2021 (slope: -0.442, p-value $= 0.002$, $R^2 = 0.27$, Figure 5.4c). There was no variation in damage between white and red grapes (slope: -0.418, p-value $= 0.602$, Supplementary materials S5.3).

Damage by insects was not well explained by any of the predictors, and it did not significantly vary with distance from the field edge, boundary types, years or grape varieties (GLMM models p-value > 0.05, $R^2 = 0.05$, Supplementary materials S5.3).

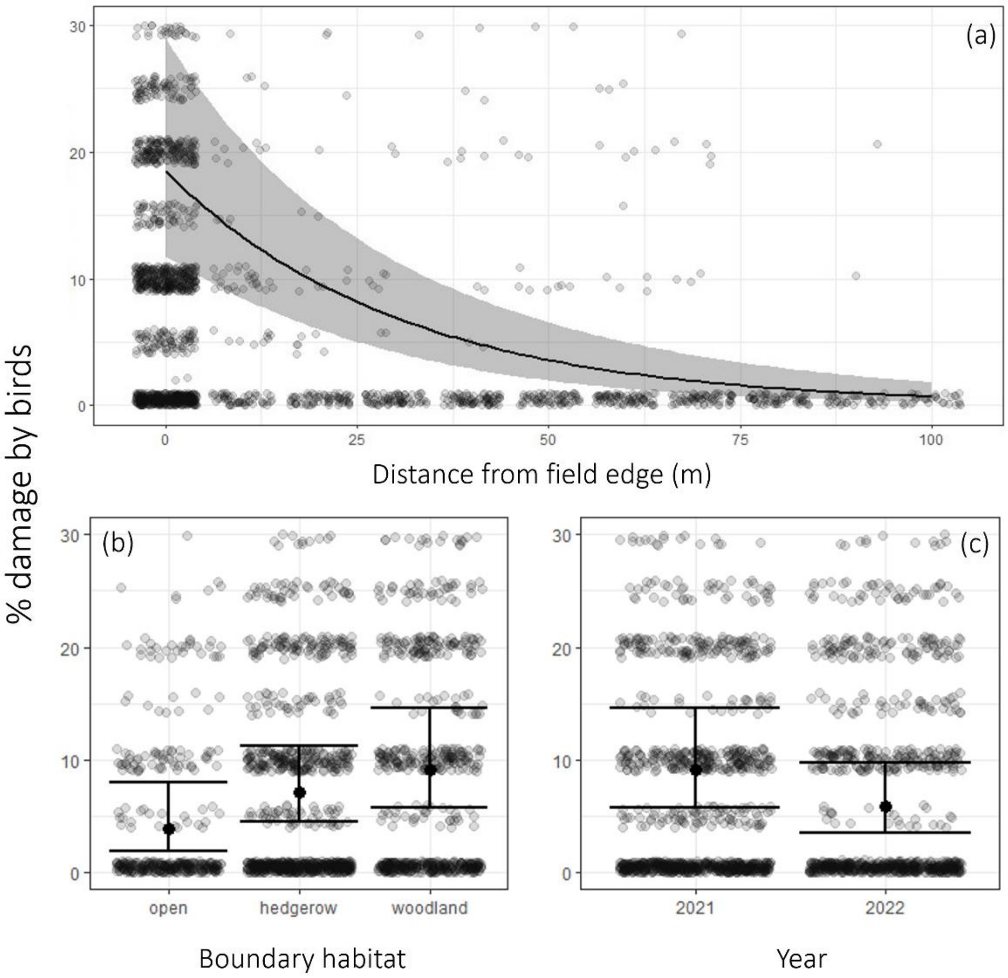


Figure 5.4. Raw values (dots) and model predicted (with 95% confidence intervals) percentage damage by birds to grape bunches (n=3,018) in relation to significant predictors of: **(a)** distance from the field edge; **(b)** boundary habitat type that surrounded the surveyed fields (hedgerow n=22, woodland n=20 and open boundary with no habitat features, n=14); and **(c)** two study years.

Exclusion experiment

Considering the control bunches only, the average damage was 2.75% by birds and 1.21% by insects. This average damage was lower than from the grape damage assessments, which included a lot of measurements from 0m, where damage was the highest. Damage by birds decreased with distance away from the field edge (average was: 6.81% at 0m, 1.26% at 30m and 0.17% at 60m), but there was little change in damage by insects (1.48%, 1.26% and 0.88%, respectively) with distance away from the edge.

Percentage of bunches damaged by birds or insects was significantly lower on '*bird-only'* exclusion (slope: 1.189, p-value < 0.001) and on '*bird + insect'* exclusion (slope: 4.814, p-value < 0.001, Figure 5.5) bunches compared to controls. Damage to bunches was also significantly lower at 30m (slope: 1.086, p-value < 0.001) and 60m (slope: 1.528, p-value < 0.001) compared to 0 m, and it was significantly lower in 2022 than in 2021 (slope: -0.494, p-value = 0.017, Figure 5.5). Damage to grape bunches did not vary with boundary type or between white and red grapes (Supplementary materials 5.3).

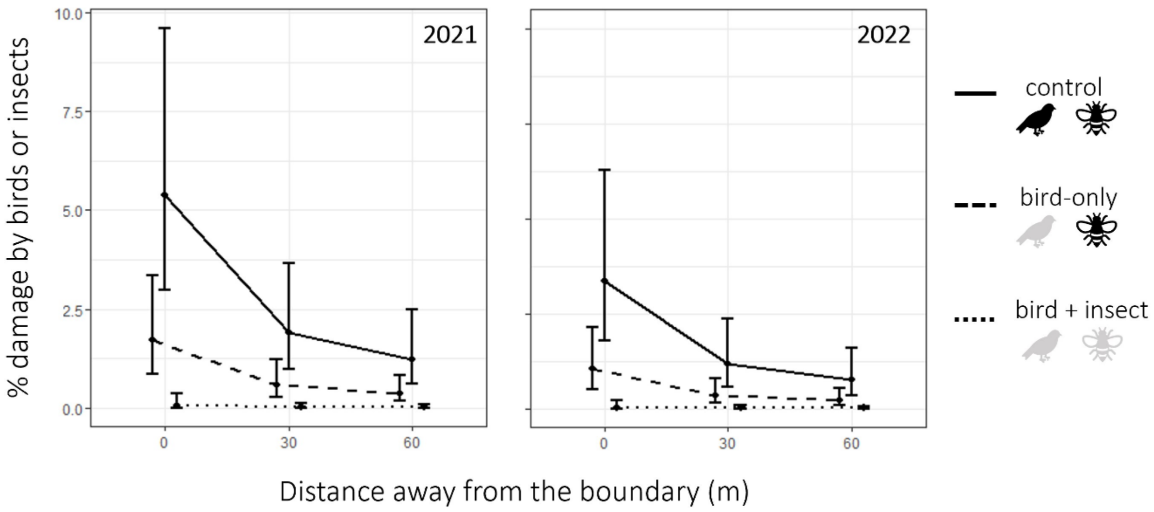


Figure 5.5. Model predicted (with 95% confidence intervals) percentage grape bunches damaged by birds or insects across three exclusion experiment treatments, at three distances from the edge of a field (in metres) and in the two study years. Exclusion experiment was performed across 47 transects in 16 English vineyards, and the three conditions were: control with no exclusion, *bird-only* exclusion and *bird + insect* exclusion, totalling 790 experimental bunches.

5.3.2. Relationship between grape damage and bird communities

In total, we recorded 5,297 birds belonging to 61 species, which included 10 carnivorous, 13 herbivorous, 15 invertivorous and 23 omnivorous species, and 16 species were considered grape-eaters (Figure 5.6). The total bird abundance was highest at harvest, when omnivorous species were most abundant (Figure 5.6a). At harvest, 62.4% of all recorded individuals were of grape-eating species, compared to 22.9% at budding and 28.4% at flowering (Figure 4.6b). The most abundant grape-eaters at harvest were Starlings *Sturnus vulgaris* (20% of total bird abundance at harvest), followed by Wood Pigeons *Columba palumbus* (10%), Goldfinches *Carduelis carduelis* (9%), Jackdaws *Corvus monedula* (7%), and Pheasants (6%). Across all seasons, we recorded 15 red-listed species (Stanbury *et al.*, 2021), which included 7 grape-eating species (Supplementary materials S5.1).

Neither the abundance of grape-eating or invertebrate-eating species at harvest was predicted by semi-natural habitat cover in the landscape surrounding the vineyards, nor by vineyard management practices, and it did not vary significantly between 2021 and 2022 (Supplementary materials 5.3). Grape damage by birds was not predicted by the total bird abundance (slope: 0.035, p-value = 0.796, Supplementary materials 5.3), but it significantly increased with increasing abundance of grape-eating bird species (slope: 0.043, p-value = 0.011, R^2 = 0.11, Figure 4.6c). Grape damage by insects was not predicted by the total bird abundance (slope: 0.003, p-value = 0.821), nor by invertebrate-eating species abundance (slope: 0.015 p-value = 0.300; Supplementary materials S5.3).

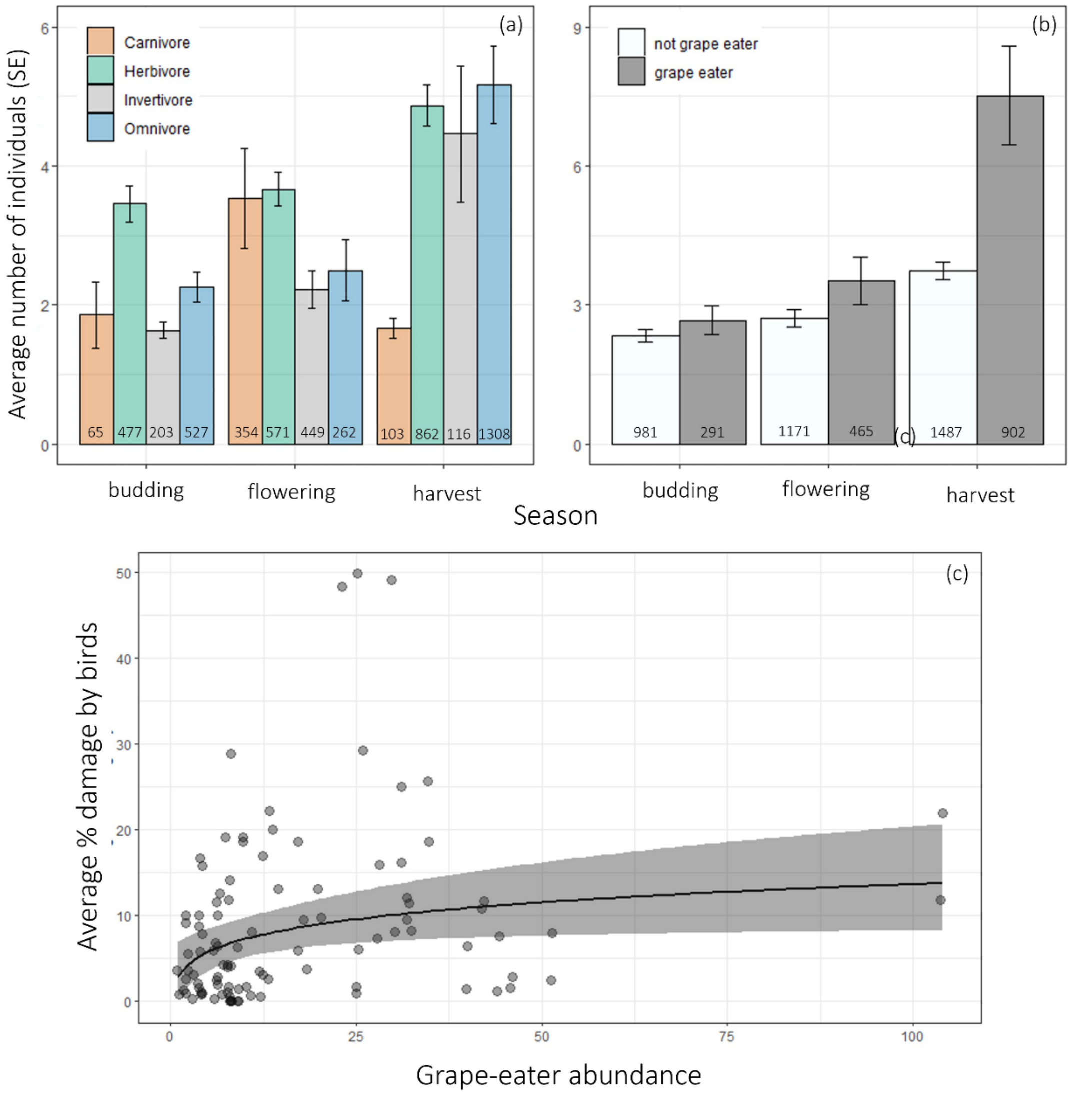


Figure 5.6. Average (± SE) abundance of birds belonging to one of the four dietary groups **(a)**, according to whether species were grape-eaters **(b)**, and raw (dots) and model predicted (with 95% confidence intervals) average percent damage to grape bunches by birds in relation to the abundance of grape-eating bird species **(c)** as recorded at the time of harvest. Bird communities were monitored through point counts in each survey field (n=28) across the 16 study vineyards, in the budding (April), flowering (June and July) and harvest (September and October) seasons in 2021 and 2022 (n=182 surveys). Total abundance of birds belonging to each dietary group is given in **(a)** and **(b;** total abundance at budding: 1,272, flowering: 1,636 and harvest: 2,389).

5.3.3. Relationship between grape damage, bird communities, yield and vineyard management

The average yield across the study vineyards and years was 4.10 ± 0.31 (SE) tonnes per hectare. Yield was significantly lower in certified-organic (3.02 ± 0.40) than non-organic (4.64 ± 0.37) vineyards (estimate: -1.364, p-value = 0.028), and significantly higher in 2022 (4.62 ± 0.48) than in 2021 (3.64 ± 0.38; estimate: 1.042, p-value = 0.037, R^2 = 0.49, Figure 5.7a). Yield did not significantly differ between non-SWGB (3.39 ± 0.42) and SWGB-accredited (4.64 ± 0.41) vineyards (Supplementary materials S5.3). Yield significantly increased with the site's *ecotoxicity score* (slope: 0.060, p-value = 0.042, R^2 = 0.50, Figure 5.7b), but it did not vary with the *ecotoxicity frequency* and *practice scores*, nor *ground vegetation cover* (Supplementary materials S5.3).

Yield was also significantly reduced by the interaction between grape-eating bird species abundance and field edge density (slope: -0.0005, p-value < 0.001, R^2=0.55), whereby there was a significant negative effect of field edge density in vineyards with a high abundance of grape-eating bird species (Figure 5.7c). Field edge density was significantly higher in certified-organic (370.0 m / ha ± 13.06 SE) than non-organic vineyards (286.5 ± 19.51; t-test: t-value = 3.555, df = 28, p-value = 0.001).

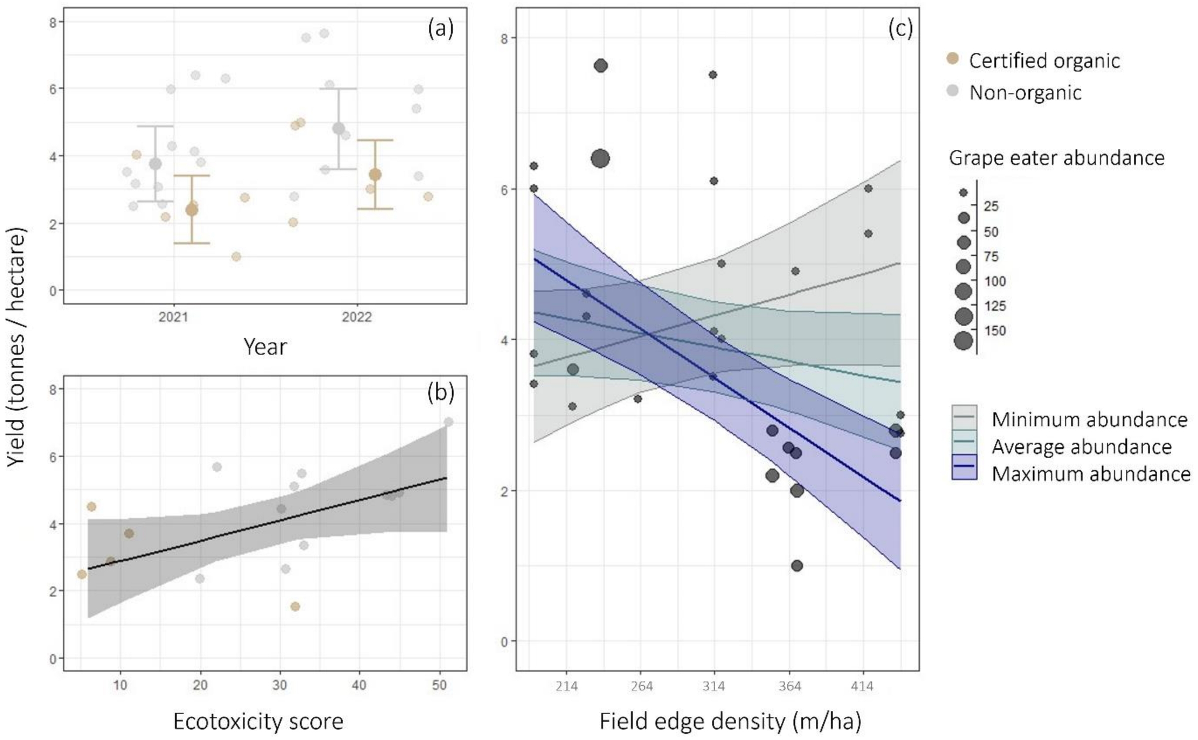


Figure 5.7. Raw (points) and model-predicted (with 95% CI) grape yield across the study vineyards (n=16) in relation to: **(a)** the two study years and whether a site was certified-organic (beige) or non-organic (grey), **(b)** each sites' average *ecotoxicity score* across the two study years, and **(c)** the interaction between field edge density and grape-eating bird species abundance. In **(c)**, the size of the points indicates the raw values for grape-eating species abundance, whilst the predictions use mean-centred values for grape-eating bird species abundance and field edge density.

5.3.4. Economic impact of bird damage at a vineyard scale

Scaling up the model estimates of spatial variation in grape damage by birds to the scale of whole fields showed that the average predicted grape damage by birds, and thus relative revenue loss per hectare, was double in the smallest vine fields (~13.45% loss across a field), compared to the largest fields (~6.78% loss; Figure 5.8). This magnitude of difference is lower than that predicted due to vineyard management or annual variation, as organic vineyards were predicted to have 36% lower yield than non-organic vineyards (decrease of 1.36 tonnes / ha equating to ~£727 / ha), whilst yield was 22% higher in 2022 than in 2021 (1.04 tonnes / ha ~ £440 / ha). The magnitude of difference based on boundary type was predicted to be the highest, as grape damage was predicted to be 42% lower in fields with open and featureless compared to woodland boundaries (for a median field, the relative loss in revenue would be ~£281 / ha).

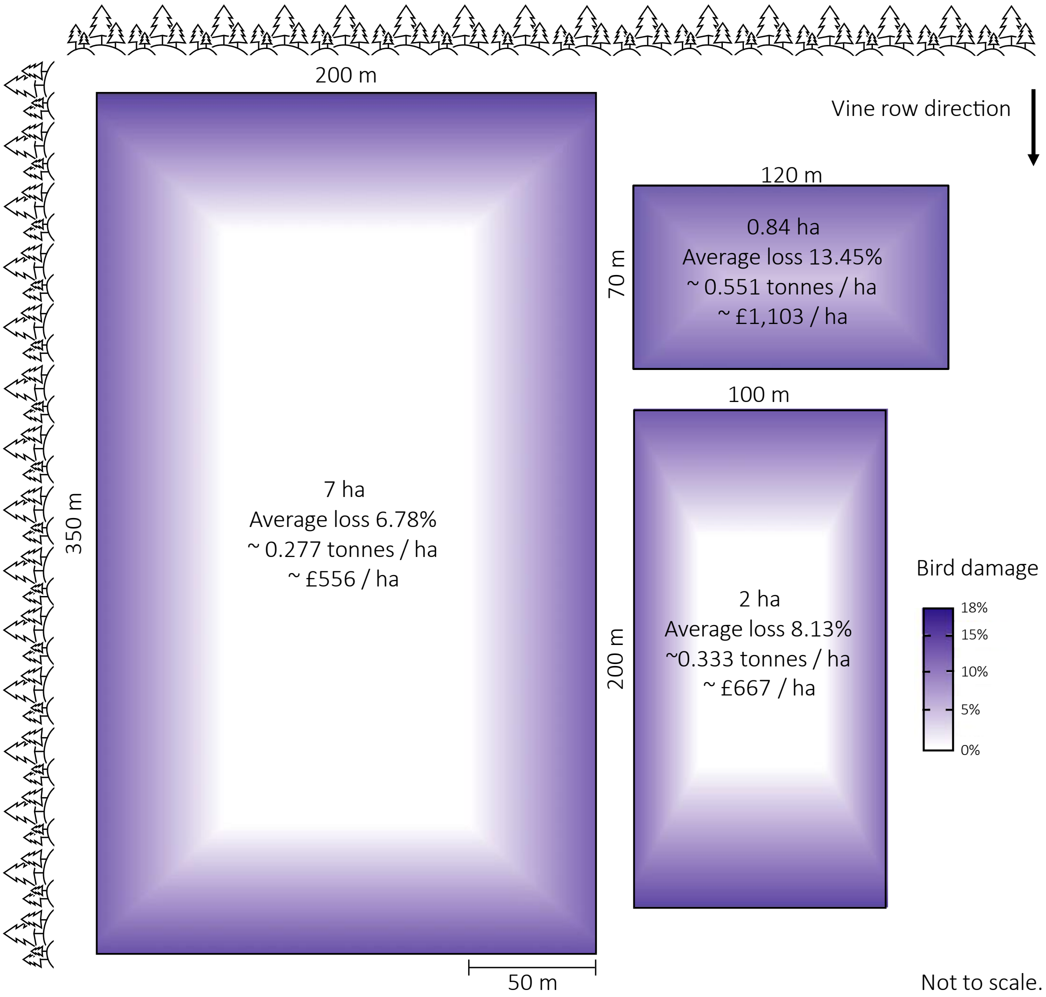


Figure 5.8. Field schematics showing predicted percent damage to grape bunches by birds in relation to the distance from field edges. Three field sizes are presented which are representative of the study vineyards, ranging from the smallest average field (0.84 ha), a median-sized field (2 ha) and the largest average field (7 ha). Predicted grape damage across each field was averaged and used to estimate the relative loss in yield and revenue, per hectare, using the expected yield of 4.1 tonnes / ha, which was the from across our study sites and study years.

5.4. Discussion

We have demonstrated that birds contribute more grape damage across English vineyards than insects and fungal disease damage, and that damage rates vary spatially, being significantly higher at field edges and fields neighbouring woodlands. We observed an influx of grape-eating species at harvest, and unsurprisingly, showed that bird damage is positively related to their abundance. However, the high abundance of grape-eaters only resulted in a significantly lower yield in vineyards with high field edge density, which can be used to inform targeted bird management. Importantly, seven of the 16 grape-eating species, such as Starlings, are also of conservation concern, which means that management of birds in vineyards needs to be handled sensitively and we propose industry sustainability schemes could offer compensation, or losses could be offset by higher product prices for accredited vineyards. Organic vineyards were found to have 35% lower yield than non-organic vineyards, which we suggest could be due to a combination of reduced vine vigour and higher average field edge density increasing the impact of bird frugivory.

5.4.1. Spatial and temporal variation in grape damage and the effect of bird communities

Animal damage across English vineyards was prevalent, occurring at 40% of grape bunches but when considering the proportion of each affected bunch that was damaged, the impact of frugivory was low. As predicted, frugivory by birds was the main source of grape losses in English vineyards, averaging 7.9%. This level of grape damage aligns with that observed across Australian vineyards (Peisley *et al.*, 2017), but is much lower than the reported rates of 20% in Californian (Kross *et al.*, 2012) and 75% in New Zealand (Fukuda *et al.*, 2008) vineyards. Unsurprisingly, the average grape damage by birds was related to the abundance of grape-eating species in vineyards, as at harvest 62% of all recorded individuals were grape-eaters. This is part-due to an influx in the numbers of grape-eaters, particularly Starlings, the most abundant grape-eater we observed, and in-part due to dietary shifts from insectivorous diets during the breeding season to more omnivorous diets (Herrmann & Anderson, 2016). We found the most abundant grape-eaters to include species of starlings, pigeons, finches and corvids, which several previous studies have also identified as fruit pests (Herrmann & Anderson, 2016; Kross *et al.*, 2012; Lamelas-López & Marco, 2021; Luck *et al.*, 2015; Monteagudo *et al.*, 2023; Shave *et al.*, 2018; Somers & Morris, 2002). We did not find the abundance of grape-eaters to be affected by landscape complexity or management practices, and in agreement with Luck *et al.* (2015) we suggest that grape-eating species act opportunistically and if they happen to exist in a given landscape, they may flock to vineyards as the fruit ripens. A caveat to this is that the increase in grape damage was not proportional to grape-eaters' abundance across our sites, as whilst grape damage was predicted to double when grape-eater abundance rose from 0 to 20 individuals, it only doubled again when the abundance increased 5-fold to over 100 individuals. This suggests that other factors modulate the relationship between grape-eater abundance and grape losses.

Grape damage by birds was highest at field edges where it averaged 18% and it significantly declined with distance away from the edge, halving every 21 metres, and it was also 42% higher next to woodland compared to open boundaries. This is likely directly caused by higher bird numbers and activity at field edges with trees (Kross *et al.*, 2012; Peisley *et al.*, 2017; Somers & Morris, 2002), which offer perching places and provide shelter from predators, however this predictable pattern eases targeting of actions to minimise bird damage (e.g. Fukuda *et al.*, 2008; Peisley *et al.*, 2017). In some cases, perching features may be more randomly distributed, as we observed across our sites where telephone wires passing over vineyard fields provided perches for Starlings (pers. obs), which we hypothesise may lead to unpredictable patterns of grape damage. Such risks should be considered in vineyard design to limit feeding opportunities to key grape-eaters, or may require more dynamic management, such as encouraging activity of birds of prey whose presence may deter frugivory at wider spatial scales (e.g. Kross *et al.*, 2012).

Landscape heterogeneity has been shown to have a positive effect on fruit production, increasing pest control and decreasing frugivory (Gonthier *et al.*, 2019; Pejchar *et al.*, 2018; Smith *et al.*, 2022; Zhang *et al.*, 2007), but we did not find the abundance of ecosystem service and disservice providing species to vary with landscape composition or on-farm management practices. Zielonka *et al.* (2023, Chapter 4) demonstrated that bird communities, and particularly bird abundance, in English vineyards are less sensitive to landscape composition and management than has been shown elsewhere (e.g. Barbaro *et al.*, 2021; Paiola *et al.*, 2020). The key grape-eating species are habitat generalists and thus adaptable to agricultural landscapes so we suspect they may be less dependent on semi-natural habitats or affected by vineyard management practices. Grape-eater numbers increased at harvest, and frugivory rates varied between the study years, suggesting that the influx of grape-eaters and their activity varies temporarily and may be driven by the availability of alternative feeding resources in the surrounding landscape. For example, frugivory rates in South African vineyards were higher in years when ripening of grapes mismatched with the availability of wild foods (Herrmann & Anderson, 2016). Vineyard harvest dates vary interannually based on climatic conditions that affect ripening, which highlights the complexity of forecasting grape damage, and we suggest managers monitor bird numbers and activity patterns to inform strategic management.

5.4.2. Relationship between grape damage, yield and vineyard management

Organic vineyards had 35% lower yield than non-organic vineyards, which we suggest could be due to a combination of reduced vine vigour and higher field edge density increasing the impact of bird frugivory. Organic vineyards in our study were characterised by smaller fields and higher field edge density, which we found to be significantly reduce yield in vineyards with a high grape-eater abundance. A strong motivator to organic management is personal concern for the environment and biodiversity (Pomarici *et al.*, 2015; Siepmann & Nicholas, 2018), thus it is likely that organic managers are more likely to limit field sizes and incorporate patches of semi-natural habitats across their vineyards to keep them more nature-friendly, but this may inflate the impact that frugivory has on yield. Importantly, organic-status and average field size, were not predictors of bird diversity or abundance across English vineyards (Zielonka *et al.*, 2023; Chapter 4), thus decreasing field edge density by planting larger fields in areas with a high abundance of grape-eaters may minimise yield losses without exerting a negative effect on the bird communities.

The difference in yield between organic and non-organic English vineyards is within the range documented across other crop systems (e.g. Seufert *et al.*, 2012), though the magnitude of this difference is highly contextual (Samnegård *et al.*, 2019), and variable across crop types (de la Cruz *et al.*, 2023). The difference in yield between organic and non-organic vineyards is likely due to a combination of direct and indirect factors. A direct driver of the difference may be related to agrochemical use, as organic vineyards have significancy lower ecotoxicity scores derived from agrochemical use data (Zielonka *et al.*, 2023; Chapter 4), whilst we found a positive relationship between ecotoxicity scores and yield. We hypothesise that vine growth may be reduced in organic vineyards due to lower vine vigour caused by reduced mineral availability (Döring *et al.*, 2015; Seufert *et al.*, 2012). In similar European organic fruit systems, higher incidence of insect pests and fungal damage was observed and linked to lower efficacy of pesticides and fungicides (e.g. Samnegård *et al.*, 2019), though this is likely less important across English vineyards where the rates of insect damage and fungal disease were low.

5.5. Synthesis and recommendations

Management of birds in vineyards poses its challenges as seven of the 16 grape-eaters are also nationally red-listed species that have undergone population declines and range reductions, and are thus, conservation priorities in the UK (Stanbury *et al.*, 2021). Non-lethal deterrents, such as gas guns and bird scarers, are commonly used in vineyards but most are not species-specific (Garcia *et al.*, 2020) and remain ineffective in the long term as birds typically habituate to them (Anderson *et al.*, 2013; Rivadeneira *et al.*, 2018; Wang *et al.*, 2019). Increasingly the focus has been shifting towards more biodiversity-friendly approaches to deter grape-eating birds, namely through the provision of perches and nest boxes to encourage predatory bird presence and activity (Kross *et al.*, 2016; Monteagudo *et al.*, 2023; Peisley *et al.*, 2017). The results are promising as predatory birds have reduced damage by as much as much as 50-85% (Kross *et al.*, 2012; Peisley *et al.*, 2017), though their effectiveness remained mixed at field edges where grape-eaters foraged the most (Monteagudo *et al.*, 2023). Vineyard homogenisation through the removal of perching and shelter habitat surrounding field edges and increasing field size could be another option to minimising grape damage by birds, though this may have negative effects on wider vineyard biodiversity (Barbaro *et al.*, 2021; Paiola *et al.*, 2020; Smith *et al.*, 2022) and could reduce soil fertility and other ecosystem services (Garcia *et al.*, 2023; Holland *et al.*, 2017). Instead, incorporating a wider grassland strip, at least 50 m wide, between boundary habitats and grape fields could both reduce grape damage, whilst promoting biodiversity, as a positive effect of ground vegetation cover has been widely noted across vineyards (Geldenhuys *et al.*, 2021; Winter *et al.*, 2018; Zielonka *et al.*, 2023, Chapter 3).

Yield is the primary concern for farmers, thus detrimental effects of organic management or bird-promoting practices could be a barrier to their uptake. It is important to note that the benefits harnessed from biodiversity stretch beyond those directly affecting the yield as vineyard landscapes can hold high cultural significance (Assandri *et al.*, 2018), and birds deliver cultural and wellbeing benefits through their song, with bird-watching being a popular activity (Gaston *et al.*, 2018; Whelan *et al.*, 2015). These ecosystem services may contribute to the overall business prosperity as vineyards are strongly associated with tourism (Sussex Modern, 2023; Chapter 6), but are rarely quantified or considered within agricultural landscape management. Sustainable management should focus on making vineyards thrive as multifunctional landscapes, but this may require stronger policy incentives or compensations. For example, compliance with industry accreditations promoting sustainable practices (e.g. SWGB, 2020) could be rewarded through higher wine retail prices, or instead the costs associated with the provision of raptor nest boxes, or the yield losses associated with retaining wooded boundaries that increase frugivory, or reducing agrochemical use to aid biodiversity conservation (Zielonka *et al.*, 2023), could be directly compensated for in payments.

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Chapter 5 – Supplementary Materials

S5.1. Bird species dietary groups

Table S5.1. List of bird species recorded in English vineyards and the feeding guilds they belong to (see details in 5.2.3.), and also indicating if they are red listed in Birds of Conservation Concern 2021 list.

Common name	Latin name	Red listed	Diet overall	Diet budding	Diet flowering	Diet harvest	Grape-eater
Barn swallow	*Hirundo rustica*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Black headed gull	*Chroicocephalus ridibundus*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Blackbird	*Turdus merula*	no	Omnivore	Omnivore	Omnivore	Omnivore	no
Blackcap	*Sylvia atricapilla*	no	Omnivore	Invertivore	Invertivore	Herbivore	no
Blue tit	*Cyanistes caeruleus*	no	Omnivore	Invertivore	Invertivore	Herbivore	no
Buzzard	*Buteo buteo*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Canada geese	*Branta canadensis*	no	Herbivore	Herbivore	Herbivore	Herbivore	no
Carrion crow	*Corvus corone*	no	Omnivore	Omnivore	Carnivore	Omnivore	no
Chaffinch	*Fringilla coelebs*	no	Omnivore	Omnivore	Omnivore	Omnivore	no
Chiffchaff	*Phylloscopus collybita*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Coal tit	*Periparus ater*	no	Omnivore	Invertivore	Invertivore	Invertivore	no
Collared dove	*Streptopelia decaocto*	no	Herbivore	Herbivore	Herbivore	Herbivore	no
Dunnock	*Prunella modularis*	no	Omnivore	Omnivore	Invertivore	Omnivore	no
Fieldfare	*Turdus pilaris*	yes	Invertivore	Invertivore	Invertivore	Omnivore	yes
Goldfinch	*Carduelis carduelis*	no	Herbivore	Herbivore	Herbivore	Herbivore	yes
Great tit	*Parus major*	no	Omnivore	Omnivore	Invertivore	Omnivore	no
Great woodpecker	*Picus viridis*	no	Omnivore	Omnivore	Omnivore	Omnivore	yes
Greenfinch	*Carduelis chloris*	yes	Herbivore	Herbivore	Herbivore	Herbivore	yes
Grey heron	*Ardea cinerea*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Grey wagtail	*Motacilla cinerea*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Herring gull	*Larus argentatus*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
House martin	*Delichon urbica*	yes	Invertivore	Invertivore	invertivore	Invertivore	no
House sparrow	*Passer domesticus*	yes	Herbivore	Herbivore	Herbivore	Herbivore	yes
Jackdaw	*Corvus monedula*	no	Omnivore	Omnivore	Invertivore	Omnivore	yes
Jay	*Garrulus glandarius*	no	Omnivore	Invertivore	Invertivore	Herbivore	yes
Kestrel	*Falco tinnunculus*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Lapwing	*Vanellus vanellus*	yes	Invertivore	Invertivore	Invertivore	Invertivore	no
Linnet	*Carduelis cannabina*	yes	Herbivore	Herbivore	Herbivore	Herbivore	no
Little owl	*Athene noctua*	no	Carnivore	Carnivore	Carnivore	Carnivore	no

Long-tailed tit	*Aegithalos caudatus*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Magpie	*Pica pica*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Mallard	*Anas platyrhynchos*	no	Herbivore	Herbivore	Herbivore	Herbivore	no
Meadow pipit	*Anthus pratensis*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Merlin	*Falco columbarius*	yes	Carnivore	Carnivore	Carnivore	Carnivore	no
Mistle thrush	*Turdus viscivorus*	yes	Omnivore	Invertivore	Invertivore	Herbivore	yes
Moorhen	*Gallinula chloropus*	no	Omnivore	Omnivore	Omnivore	Omnivore	no
Nuthatch	*Sitta europaea*	no	Invertivore	Invertivore	Invertivore	Omnivore	no
Pheasant	*Phasianus colchicus*	no	Herbivore	Herbivore	Herbivore	Herbivore	yes
Pied wagtail	*Motacilla alba*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Raven	*Corvus corax*	no	Omnivore	Omnivore	Carnivore	Omnivore	no
Red kite	*Milvus milvus*	no	Omnivore	Carnivore	Carnivore	Carnivore	no
Red legged partridge	*Alectoris rufa*	no	Herbivore	Herbivore	Herbivore	Herbivore	yes
Redpoll	*Cardeulis flammea*	yes	Herbivore	Herbivore	Herbivore	Herbivore	no
Redstart	*Phoenicurus phoenicurus*	no	Invertivore	Invertivore	Invertivore	Invertivore	yes
Redwing	*Turdus iliacus*	yes	Omnivore	Invertivore	Invertivore	Omnivore	yes
Robin	*Erithacus rubecula*	no	Omnivore	Omnivore	Invertivore	Omnivore	no
Rook	*Corvus frugilegus*	no	Omnivore	Omnivore	Omnivore	Herbivore	yes
Skylark	*Alauda arvensis*	yes	Omnivore	Omnivore	Invertivore	Omnivore	no
Snipe	*Gallinago gallinago*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Song thrush	*Turdus philomelos*	yes	Omnivore	Omnivore	Omnivore	Omnivore	yes
Sparrowhawk	*Accipiter nisus*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Starling	*Sturnus vulgaris*	yes	Omnivore	Omnivore	Invertivore	Omnivore	yes
Stock dove	*Columba oenas*	no	Herbivore	Herbivore	Herbivore	Herbivore	no
Swift	*Apus apus*	yes	Invertivore	Invertivore	Invertivore	Invertivore	no
Tawny owl	*Strix aluco*	no	Carnivore	Carnivore	Carnivore	Carnivore	no
Treecreeper	*Certhia familiaris*	no	Invertivore	Invertivore	Invertivore	Invertivore	no
Whitethroat	*Sylvia communis*	no	Omnivore	Invertivore	invertivore	omnivore	no
Wood Pigeon	*Columba palumbus*	no	Herbivore	Herbivore	Herbivore	Herbivore	yes
Wren	*Troglodytes troglodytes*	no	Omnivore	Omnivore	Invertivore	Omnivore	no
Yellowhammer	*Emberiza citrinella*	yes	Herbivore	Herbivore	Omnivore	Herbivore	no

S5.2. Description of response and exploratory variables and model structure

Type	Variable	Distribution	Description
Response	Grape damage by birds	Binomial (logit)	Proportion of grapes in a bunch that were damaged by birds
	Grape damage by insects	Binomial (logit)	Proportion of grapes in a bunch that were damaged by insects
	Grape damage by birds + insects (from exclusion experiment)	Beta-binomial (logit)	Proportion of grapes in a bunch that were damaged by birds or insects
	Yield	Gaussian (identity)	Average grape yield in tonnes per hectare for each study site and year
Response / explanatory	Grape-eating bird species abundance	Gaussian (logit)	Number of individuals of grape-eating bird species recorded in each survey field and year
	Invertebrate-eating bird species abundance	Gaussian (logit)	Number of individuals of invertebrate-eating bird species (invertivores + omnivores) recorded in each survey field and year
	Average grape damage by birds	Binomial (logit)	Proportion of grapes in a bunch that were damaged by birds averaged per field and year
	Average grape damage by insects	Binomial (logit)	Proportion of grapes in a bunch that were damaged by insect averaged per field and year
Exploratory	Boundary habitat	Categorical 3 levels	Boundary habitats surrounding vine fields: woodland, hedgerows or open-boundary lacking any habitat features
	Year	Categorical 2 levels	2021 or 2022
	Grape variety	Categorical 2 levels	White or red
	Distance from field edge (m)	Categorical 3 levels	Exclusion experiment only - distance away from field edge: 0, 30 or 60 m
	Distance from field edge (m)	Continuous (1-100m)	Grape damage assessments only - distance away from field edge
	Exclusion treatment	Categorical 3 levels	Control, bird-only and bird+insect exclusion
	Ecotoxicity score	Continuous	Environmental toxicity score derived from agrochemical use
	Ecotoxicity frequency score	Continuous	Ecotoxicity score multiplied by agrochemical application frequency
	Practice score	Continuous	Score for vineyard management practices based on how detrimental or beneficial they are for biodiversity conservation
	Ground vegetation cover	Continuous	Metric based on proportion ground covered by vegetation and vegetation height as measured along survey transects in between vine rows in each field and year

	Field edge density (m / ha)	Continuous	Total vine field perimeter length divided by hectares of planted vines at each site
	SNH-cover	Continuous	Proportion cover by woodland and semi-natural grasslands in a 2.5 km radius buffer around each site
	Certified-organic status	Categorical 2 levels	Certified organic or non-organic
	SWGB-accreditation status	Categorical 2 levels	SWGB-accredited or non-SWGB
	Total bird abundance	Continuous	Total number of bird individuals recorded in each survey field and year
Random	Field ID / Vineyard	28-level categorical factor / 16-level categorical factor	Unique identifier of survey fields (n=28) across 16 sites
	Transect ID / Vineyard	47-level categorical factor / 16-level categorical factor	Unique identifier of each exclusion experiment transect (n=47) across 16 sites
	Vineyard	16-level categorical factor	Unique identifier for each of the 16 sites

Response	Model Structure
Spatial and temporal variation in grape damage by birds and insects - grape assessments	
Grape damage by birds	Distance from field edge + Boundary + Year + Grape Variety + (1|Field ID / Vineyard)
Grape damage by insect	Distance from field edge + Boundary + Year + Grape Variety + (1|Field ID / Vineyard)
Spatial and temporal variation in grape damage by birds and insects - exclusion experiments	
Grape damage by birds + insects	Exclusion treatment + Boundary + Distance from field edge + Year + Grape Variety + (1| Transect ID / Vineyard)
Relationship between grape damage and bird communities	
Average grape damage by birds	Total bird abundance + Year + (1|Field ID / Vineyard)
Average grape damage by birds	Grape-eating bird species abundance + Year + (1|Field ID / Vineyard)
Average grape damage by insects	Total bird abundance + Year + (1|Field ID / Vineyard)
Average grape damage by insects	Invertebrate-eating bird species abundance + Year + (1|Field ID / Vineyard)
Grape-eating bird species abundance	SNH-cover + ecotoxicity score + ecotoxicity frequency score + practice score + ground vegetation volume + year + (1|Field ID / Vineyard)
Invertebrate-eating bird species abundance	SNH-cover + ecotoxicity score + ecotoxicity frequency score + practice score + ground vegetation volume + year + (1|Field ID / Vineyard)
Relationship between grape damage, bird communities and yield	
Yield	Grape-eating bird species abundance + field edge density + Grape-eating bird species abundance * field edge density + Year + (1|Vineyard)
Yield	Certified-organic status + SWGB-accreditation status + Year + (1|Vineyard)
Yield	Ecotoxicity score + ecotoxicity frequency score + practice score + ground vegetation volume + (1|Vineyard)

S5.3. Model outputs

Table S5.3. Modelled effects (and 95% confidence intervals) of semi-natural habitat features, study year, grape variety, vineyard management predictors bird abundance on the proportion of grapes damaged by birds and insects, with reported conditional standard error (Cond. SE), t-value, p-value, and Akaike Information Criterion (AIC). See S5.2. for details about variables. Significant effects (when estimates with 95% CI do not span zero, and p < 0.05) are highlighted in blue.

Response	Variable	Estimate	Std. Error	z-value	p-value	AIC	mR2
Spatial and temporal variation in grape damage by birds and insects - grape assessments							
Grape damage by birds	Intercept	-2.559	0.365	-7.012	<0.001	1374.9	0.276
	Distance from the edge	-0.033	0.005	-7.206	<0.001		
	Boundary: hedge	0.614	0.390	1.574	0.116		
	Boundary: woodland	0.870	0.400	2.175	0.030		
	Year 2022	-0.442	0.140	-3.167	0.002		
	Variety - white	-0.418	0.228	1.835	0.066		
Grape damage by insects	Intercept	-4.451	0.538	-8.280	<0.001	303.5	0.058
	Distance from the edge	-0.006	0.008	-0.851	0.395		
	Boundary: hedge	-0.572	0.573	-0.997	0.319		
	Boundary: woodland	0.295	0.526	0.561	0.575		
	Year 2022	-0.102	0.408	-0.251	0.802		
	Variety - white	-0.160	0.416	-0.384	0.701		
Spatial and temporal variation in grape damage by birds and insects - exclusion experiments							
Grape damage by birds + insects	Intercept	2.853	0.370	7.705	<0.001	1286.3	0.832
	Bird only exclusion	1.189	0.220	5.402	<0.001		
	Bird + insect exclusion	4.814	1.009	4.772	<0.001		
	Boundary: hedgerow	0.202	0.352	0.574	0.566		
	Boundary: woodland	-0.275	0.358	-0.768	0.443		
	Distance 30 m	1.086	0.239	4.536	<0.001		
	Distance 60 m	1.528	0.266	5.748	<0.001		
	Year 2022	-0.494	0.206	-2.397	0.017		
	Variety - white	0.303	0.282	1.076	0.282		
Relationship between grape damage and bird communities							
Grape-eating bird species abundance	Intercept	3.508	1.014	3.459	<0.001	133.8	0.167
	SNH cover	-1.737	2.929	-0.593	0.553		
	Ecotoxicity score	0.001	0.017	0.054	0.957		
	Ecotoxicity frequency score	-0.013	0.012	-1.114	0.265		
	Practice score	0.123	0.068	1.807	0.071		
	Ground vegetation volume	0.002	0.070	0.026	0.979		
	Year 2022	-0.347	0.241	-1.438	0.151		
Invertebrate-eating bird species abundance	Intercept	2.635	0.635	4.149	<0.001	103.1	0.115
	SNH cover	1.055	1.832	0.576	0.565		
	Ecotoxicity score	0.012	0.011	1.092	0.275		
	Ecotoxicity frequency score	-0.005	0.008	-0.697	0.486		
	Practice score	0.044	0.043	1.031	0.302		
	Ground vegetation volume	0.047	0.044	1.076	0.282		
	Year 2022	-0.297	0.180	-1.645	0.100		

Average grape damage by birds	Intercept	0.147	0.114	2.853	0.292	-93.3	0.044
	Year 2022	-0.049	0.018	1.179	0.065		
	Total bird abundance	0.035	0.030	0.259	0.340		
Average grape damage by birds	Intercept	0.170	0.048	3.533	<0.001	-98.3	0.11
	Year 2022	-0.039	0.026	-1.482	0.138		
	Grape-eating species abundance	0.043	0.017	2.537	0.011		
Average grape damage by insects	Intercept	-6.465	0.728	-8.884	<0.001	452.1	0.033
	Year 2022	-0.865	0.429	-2.016	0.044		
	Total bird abundance	0.003	0.014	0.226	0.821		
Average grape damage by insects	Intercept	-6.759	0.558	-12.105	<0.001	467.5	0.044
	Year 2022	-0.766	0.432	-1.771	0.077		
	Invertebrate-eating species abundance	0.015	0.014	1.036	0.300		
Relationship between grape damage, bird communities, yield and vineyard management							
Yield	Intercept	3.9017	0.3039	12.838	<0.001	104.5	0.55
	Year 2022	0.9385	0.4197	2.236	0.025		
	Field edge density	-0.0038	0.0026	-1.431	0.152		
	Grape-eating bird abundance	-0.0231	0.0087	-2.667	0.008		
	Field edge density * Grape-eating bird abundance	-0.0005	0.0001	-4.513	<0.001		
Yield	Intercept	3.743	0.575	6.507	<0.001	113.7	0.489
	Year 2022	1.042	0.500	2.086	0.037		
	SWGB accredited	0.570	0.590	0.967	0.334		
	Certified organic	-1.364	0.620	-2.198	0.028		
Yield	Intercept	0.644	1.776	0.362	0.717	52.8	0.50
	Ecotoxicity score	0.060	0.031	1.941	0.042		
	Ecotoxicity frequency score	0.012	0.023	0.510	0.610		
	Practice score	-0.210	0.132	-1.588	0.112		
	Ground vegetation volume	0.140	0.130	1.079	0.281		

Chapter 6: Louder and more complex vineyard soundscapes, associated with higher bird species richness, increase visitors' tour experience.

© Natalia Zielonka: Chaffinch *Fringilla coelebs* sitting on vineyard trellis, in Cambridgeshire, England.

Natalia B. Zielonka[a], Victoria Tubman[a], Lynn V. Dicks[a,b*] & Simon J. Butler[a*]

[a] School of Biological Sciences, University of East Anglia, Norwich, UK, NR4 7TJ
[b] Department of Zoology, University of Cambridge, UK, CB2 3EJ

* *joint last authors*

Abstract

1. Biodiversity is rapidly declining, reducing the quantity and quality of human interactions with nature and constraining its contribution to human health and wellbeing. Natural sounds are a key component of our experience of nature, but biodiversity losses are reflected in soundscapes, which are becoming less diverse and quieter.
2. We characterised the soundscapes across 21 English vineyards using acoustic indices and related them to bird species richness and abundance. We found that higher bird species richness, but not abundance, led to more diverse and louder soundscapes, as reflected in higher values of Acoustic Complexity Index (ACI), Bioacoustic Index (BIO) and Normalised Difference Soundscape Index (NDSI), and lower values of Acoustic Entropy Index (H).
3. Secondly, at three of the study vineyards that run vineyard tours, we measured visitors' experience of the tour in terms of *nature connectedness, vineyard perception* and *tour satisfaction*, and related these to ambient and experimentally enhanced soundscapes, where we used playback recordings of five additional birdsongs to increase the soundscapes' complexity and volume.
4. Under ambient soundscapes, participants' (n=107) experience was significantly related to higher ACI and BIO values, and lower H and Acoustic Diversity Index (ADI) values, indicating a positive effect of more diverse and louder soundscapes associated with higher bird richness.
5. Under experimental soundscape enhancement, participants (n=79) reported hearing significantly more bird species during the tour, and they reported significantly higher scores for *nature connectedness* and *vineyard perception* than under the ambient soundscape. This reinforces the direct effect of aural modality in our experience of nature.
6. Our study reinforces that: (i) the delivery of biodiversity conservation measures aimed at supporting bird diversity could simultaneously enhance the experience and wellbeing benefits of spending time in nature; and (ii) soundscapes should be protected as natural capital, and as they contribute to our wellbeing, they should be incorporated into existing

conservation policy and their conservation could be supported through existing agri-environmental and sustainability schemes.

Acknowledgements

We sincerely thank our study vineyards' managers and employees for access to field sites, in-field logistics, for providing management information, and their support and interest in our research. We thank WineGB and SWGB, and Chris Foss in particular, for their help in setting up this project and for supporting our research. Natalia Zielonka was funded by the UKRI Biotechnology and Biological Sciences Research Council Norwich Research Park Biosciences Doctoral Training Partnership [Grant number BB/M011216/1], and Victoria Tubman was supported through the University of East Anglia and Sustainable Wine of Great Britain scholarship.

6.1. Introduction

The Anthropocene is characterised by continual and pervasive biodiversity declines (Díaz *et al.*, 2019; IPBES, 2019), and together with the growing urbanisation and changing lifestyles, which have become increasingly sedentary, this has reduced the likelihood of human interactions with nature (Díaz *et al.*, 2015; Klepeis *et al.*, 2001; Soga and Gaston, 2016). Human disconnect from nature is growing and fuelling the 'extinction of experience' (Cox and Gaston, 2018; Gaston and Soga, 2020), which lessens nature's contributions to our physical and psychological health and culture (Bratman *et al.*, 2019; Gaston and Soga, 2020; IPBES, 2019), with potentially serious consequences for human health and wellbeing. For example, interactions with nature lower our risk of developing cardiovascular and respiratory diseases (Richardson and Mitchell, 2010), diabetes (Astell-Burt and Feng, 2019), and can benefit our mental wellbeing and happiness (Capaldi *et al.*, 2014; Engemann *et al.*, 2019; Joye and Bolderdijk, 2015). In fact, these benefits have been so well demonstrated that health professionals started prescribing 'time in nature' as part of treatment plans (NHS England, n.d.), and the British Government has set out a vision for 'green recovery' following the coronavirus pandemic (DEFRA, 2020).

Natural sounds are a key component of our interactions with nature (Buckley, 2022; Pijanowski *et al.*, 2011). Laboratory studies showed that sound affects our perception of landscapes (Douglas and Evans, 2022), and that listening to natural sounds leads to greater mood recovery (Benfield *et al.*, 2014) and perceived restoration (Smalley *et al.*, 2022). Birdsong is a dominant component of natural soundscapes, particularly in temperate regions (Gasc *et al.*, 2017; Uebel *et al.*, 2021), and birdsong diversity has been shown to influence our appreciation of landscapes (Hedblom *et al.*, 2014), and perceived restoration and wellbeing (Fisher *et al.*, 2021). Ferraro *et al.* (2020) showed that the experimental enhancement of natural soundscapes using playback of constructed birdsong choruses along hiking routes delivered higher levels of self-reported psychological restoration in hikers. However, a similar laboratory-based study failed to find an improvement in self-reported restoration following a playback of high avian diversity soundscape (Douglas and Evans, 2022), suggesting that perhaps the effects of sounds and the sight of natural landscape interact to deliver wellbeing benefits. The staggering and ongoing declines of bird populations and concurrent homogenisation of assemblages (Burns *et al.*, 2021; Johnson *et al.*, 2017; Olden *et al.*, 2004; Rosenberg *et al.*, 2019), translate to reductions in bird song abundance and diversity, and underpin reported large-scale declines in natural soundscape quality (Morrison *et al.* 2021), with associated implications for derived health and well-being benefits.

Farmland bird species have experienced some of the largest population declines (Inger *et al.*, 2015; Reif and Vermouzek, 2019; Rigal *et al.*, 2023). In the United Kingdom, the State of Nature 2023 Report stated that 43% of bird species are threatened with extinction, based on national IUCN red list assessments (Burns *et al.*, 2023), whilst the Farmland Bird Index shows 60% decline since its 1970 value (DEFRA, 2022). Viticulture is the UK's fastest growing agricultural sector, attributed to global warming improving the climate for grape growing (Nesbitt *et al.*, 2019). European vineyards have been shown to have detrimental effects on bird (Assandri *et al.*, 2016; Pithon *et al.*, 2016), and wider diversity (e.g. Geldenhuys *et al.*, 2022). These biodiversity responses are significantly affected by vineyard practices (Paiola *et al.*, 2020; Zielonka *et al.*, 2023 Chapter 4), but evidence-based management have been show to support high abundances of threatened and endemic avifauna within vineyards (Brambilla *et al.*, 2017).

Though fundamentally agricultural systems, vineyards are associated with tourism through vineyard tours and tastings events, with tourism contributing 24% of the total revenue across the industry (WineGB, 2023). Earlier this year, Sussex Modern, funded by the UK Government, launched a plan to support the development of the wine tourism industry, which it is estimating could be worth £658 million by 2040 and contribute over 26% to the local tourism industry (Sussex Modern, 2023). Soundscapes are an important part of the tourism experience (e.g. Fesenko and García-Rosell, 2019), where higher sound complexity has been shown to correlate positively with improved wellbeing (Fisher *et al.*, 2021), whilst positive soundscape perception has been linked to higher tourism loyalty (Jiang and Yan, 2022). This presents an opportunity for informing how soundscape conservation could support the development of vineyard tourism and contribute to the wider industry goals of sustainability and protection of the local landscapes and livelihoods (Sussex Modern, 2023; SWGB, 2020).

Here we investigated the relationship between bird diversity and soundscape characteristics, and then linked these to visitors' experience and perception of the landscape to further our understanding of the role that soundscapes play in affecting human wellbeing. Our aims were to: (1) quantify the relationships between bird diversity metrics and acoustic indices; (2) relate acoustic indices to visitors' experience of vineyard tours in relation to ambient soundscapes; (3) test whether experimental soundscape enhancement affected visitors' perception of vineyards' biodiversity; and (4) test whether experimental soundscape enhancement affected visitors' experience of the vineyard tour. We predicted that bird diversity would be reflected in acoustic indices, and that visitors' experience would be related to soundscape characteristics. We predicted that visitors subjected to soundscape enhancement would perceive the vineyards' biodiversity as being higher, and report improved tour experience.

6.2. Methods and materials

6.2.1. *Bird diversity and acoustic monitoring*

We performed acoustic monitoring and bird surveys across 21 English vineyards in 2021 and 2022. In each year, data collection took place across the three key seasons of the vine lifecycle: ‘budding’ (April-May), ‘flowering’ (June-August), and ‘harvest’ (September-October). We performed monitoring at 32 locations across the 21 vineyards, with 1-3 sampling locations per site (average 1.6 ± 0.15 SE) according to vineyard size. Sampling locations were within vine fields, at least 50 m from boundary habitats and a minimum of 250 m apart.

Active bird surveys

Bird communities in vineyards were assessed with 10-minute point counts. At each monitoring location (n=32), we performed one point count in each of the ‘budding’, ‘flowering’ and ‘harvest’ seasons in 2021 and in 2022. Point count surveys were conducted between 05:00 – 09:00 and within 3 hours of sunrise, which varied between the sampling seasons. Surveys only took place on dry and still days (Bibby *et al.*, 2000), and were performed by the same observer.

Acoustic data

At the same monitoring locations as covered by bird surveys, we recorded soundscapes using AudioMoths (Hill *et al.*, 2019), with the sampling rate set to 96 kHz and medium gain. Ten-minute recordings were taken on the hour between 05:00 – 07:10 (‘morning period’) and 18:00 – 20:10 (‘evening period’) each day, when bird vocal activity was expected to be highest, giving six 10-minute recordings in each 24-hour period. AudioMoths were placed in clear plastic bags and mounted to metal trellis poles present across all vineyards, at the height of 2metres, with the microphone facing up. This placement ensured that AudioMoths were placed above the vine canopy cover, which could obstruct the clarity of recordings. Devices were deployed twice each year, firstly at ‘budding’, and then re-deployed at ‘flowering’, before being collected at ‘harvest’.

Recordings were collected between 13th April – 11th June and 28th June – 18th September in 2021 (1,553 recording days and 9,039 10-minute recordings), and between 2nd April – 16th July 2022 (915 recording days and 5,009 ten-minute recordings). We did not make any recordings beyond 16th July in 2022 as all devices failed due to the extreme heat (Kendon, 2022). On average, data were collected on 50.15 recording days ± 1.90 SE per device and per deployment in each year and was mostly dependent on battery life. Over the two years, 8 devices were either lost or destroyed.

All sound file processing was performed in R 4.3.0 (R Core Team, 2021). Using the package *seewave* (Sueur *et al.*, 2008), we down-sampled the recordings to 44.1 kHz (following Bradfer-Lawrence *et al.*, 2019) and split the 10-minute recordings to 1-minute sub-samples. Using the packages *seewave* and *soundecology* (Sueur *et al.*, 2008; Villanueva-Rivera and Pijanowski, 2018), we quantified soundscapes using five commonly used indices that capture a range of acoustic characteristics and have been found to be reflective of biodiversity (Alcocer *et al.*, 2022). Specifically, we calculated Acoustic Complexity Index (ACI, Pieretti *et al.*, 2011), where higher values indicate higher variation in acoustic energy across frequencies and time; Acoustic Diversity Index (ADI, Villanueva-Rivera *et al.*, 2011), where higher values indicate greater acoustic evenness (arising from either a ’full’ or an ’empty’ soundscape); Bioacoustic Index (BIO, Boelman *et al.*, 2007), where higher values indicate higher variation between loud and quiet frequencies; Acoustic Entropy Index (H, Sueur *et al.*, 2008), where values towards 0 indicate a pure tone, and they increase positively with higher heterogeneity of noise towards 1, which indicates random noise; and Normalised Difference Soundscape Index (NDSI, Kasten *et al.*, 2012), where higher values indicate higher levels of biophony compared to anthrophony. Indices were computed separately for each one-minute sub-sample and using the default settings (as specified in *seewave* and *soundecology* R packages; Sueur *et al.*, 2008; Villanueva-Rivera and Pijanowski, 2018). To facilitate cross-site and cross-index comparison, all indices were standardised prior to analyses (Bradfer-Lawerence *et al.* 2020): values of ACI, ADI, H and BIO were divided by the maximum value for each index across all recordings to give relative proportions, whilst NDSI, which is on a scale from -1 to +1, was standardised by (NDSI+1)/2 (following Fairbrass *et al.*, 2017). Following standardisation, and for each acoustic index in turn, we calculated: (1) the median value across one-minute sub-samples of each 10 minute recording, and (2) the average of these for each season at each sampling location, and separately for the morning and evening periods (Bradfer-Lawrence *et al.*, 2020; Fuller *et al.*, 2015).

6.2.2. Effects of soundscape on vineyard visitors' experience

We measured visitors' experience in relation to the soundscape they experienced during vineyard tours at three of our study sites. Data collection occurred between 14th May and 2nd July 2022, which overlapped with the 'flowering' season and main vineyard tour period. Following Ferraro *et al.*, (2020), we manipulated the soundscape experienced by visitors in experimental trials, where in 'off' trials, visitors experienced the ambient soundscape, and in 'on' trials we used audio playback to enhance the soundscape. We ran these trials across 24 vineyard tours (average 7.67 per site, range 6-11), which included 12 'off' trials and 12 'on' trials, with at least three repeats of each trial condition per site. Across all trials, tours followed each vineyards' usual tour route and duration (45-60 minutes), which varied between sites but remained the same across tours at each site. This study was conducted with approval from the University of East Anglia Research Ethics Committee (ETH2122-1782).

Soundscape enhancement

We constructed our playback sound files using birdsongs of species non-native to the UK to reduce the potential disturbance of playback to breeding native species in vineyards, but we chose songs resembling common UK vineyard birds as it was important that the playback blended in within the natural soundscape. We downloaded high quality recordings (Quality = A; Type = Song) for five species: American goldfinch (*Spinus tristis,* XC169065), American robin (*Turdus* *migratorius,* XC293029), Black-capped chickadee (*Poecile atricapillus,* XC465052), Carolina wren (*Thryothorus ludovicianus,* XC248139) and Citrine wagtail (*Motacilla citreola,* XC643079) from an online database (www.xeno-canto.org). The species recordings were overlaid with random start times into an 8 minute 51 seconds (maximum duration of the five downloaded sound files) soundscape using the software GarangeBand (version 10.4.5), and saved as an .mp3 file.

We concealed a pair of WAVE A1 and A2 Portable Bluetooth speakers 15-30 m either side of the tour route at two points (at least 180 m apart) where the guides regularly paused to speak to the visitors about viticulture. We used a Decibel X:dB Sound Level Meter (Version 9.4.0) to consistently set the playback at 80dB. Playback of constructed soundscapes was initiated before tours assigned to enhanced soundscape ('on') trials began, with speakers set to loop playback of the constructed soundscape continuously. Tour guides were asked not to draw attention to the playback recordings, nor to make direct inferences about birds found across the vineyard.

Questionnaire

At the end of each tour, the tour guide invited visitors to complete our anonymous questionnaire about their vineyard experience. Participation was voluntary and interested visitors were given an information sheet, asked to give consent and were debriefed afterwards (see Supplementary Material 1). We measured the effect of the soundscape in terms of three aspects of visitors' experience: '*vineyard perception*', '*tour satisfaction*' and '*nature connectedness*'. We also collected information on participants' gender and age for descriptive purposes, and asked about their nature-related interests, which may have affected engagement with the soundscape during the tour (Capaldi *et al.*, 2014; Douglas and Evans, 2022). The full questionnaire is available in Supplementary Material S6.1.

To measure the effect of the soundscape on participants' experience, we devised 15 questions following Ferraro *et al.* (2020) and Payne (2013), which focused on characterising aspects of the soundscape that may provide psychological restoration. Five questions measured participants' fascination with the vineyard's soundscape (termed '*vineyard perception'*), five questions focussed on participants' enjoyment and wellbeing during the tour (termed '*tour satisfaction'*) and five questions measured how much participants connected with nature during the tour (termed '*nature connectedness'*). Responses were recorded on a 5-point Likert scale, where 1 = strongly disagree, and 5 = strongly agree. We also asked participants how many bird species they heard during the vineyard tour to measure their perceptions of bird diversity. For *nature connectedness* and *vineyard perception*, the mean scores from their five associated questions were used in subsequent analyses (*nature connectedness*: Cronbach's α = 0.821, 95% CI 0.771-0.860; *vineyard perception:* Cronbach's α = 0.859, 0.814-0.890; calculated using *ltm* packge in R; Rizopoulos, 2006). Responses to the five questions associated with *tour satisfaction* were less consistent (Cronbach's α = 0.681). However, excluding responses to '*The natural sounds on the tour today were overwhelming and hindered my experience'* increased reliability (α = 0.789, 0.703-0.848) and the mean of the remaining four questions for this aspect was used in subsequent analyses.

6.2.3. Statistical analyses

All statistical analyses were performed in R 4.3.0 (R Core Team, 2021) and general(ized) linear mixed models were fitted using the *glmmTMB* package (Brooks *et al.*, 2017). We firstly modelled the five acoustic indices as response variables in relation to bird species richness and total abundance. We fitted these models specifying a beta distribution, which is suitable for continuous data bound between 0 and 1 and, because it makes no prior assumptions of distribution, for skewed and heteroskedastic data (Bradfer-Lawrence *et al.*, 2020; Ferrari and Cribari-Neto, 2004). Across the models, we fitted the recording time (morning or evening) as a fixed effect and included interactions between recording time and (i) bird species richness and (ii) abundance. Deployment season ('budding', 'flowering' or 'harvest' in 2021 or 2022; 6 levels) and sampling location ID (32 levels) nested in Site ID (21 levels) were included as random effects to account for potential spatial and temporal autocorrelation. We were not able to model deployment season as a fixed effect due to uneven sampling across the seasons. Species richness and abundance were not collinear, hence we included them in the same model.

To understand which soundscape characteristics affect visitors' experience, we first fitted *vineyard perception, tour satisfaction* and *nature connectedness* scores from 'off' trials (n=107 responses) as response variables in linear mixed models and related them to each of the five acoustic indices. We used acoustic indices from 'flowering' season recordings only, as this is when the majority of tours occurred, and averaged them across 'morning' and 'evening' periods for each site. Secondly, using participants' scores from across both experimental conditions as response variables, we fitted linear mixed models that tested for the effect of soundscape enhancement on participants' experience. Here, we modelled *vineyard perception, tour satisfaction* and *nature connectedness* scores as response variables and included the treatment condition ('on' or 'off', 2 levels) as a fixed effect. All models also included Tour group ID (n=24) nested in Site ID (3 levels) as a random effect. Model residuals were normally distributed, thus Gaussian error distributions were employed in all models. We proceeded with full models, interpreting predictor significance based on whether the model estimates with 95% confidence intervals passed zero, and if $p < 0.05$.

6.3. Results

6.3.1. *Relationships between bird diversity and acoustic indices*

In total, we recorded 5,731 individuals belonging to 58 species. The average bird species richness per survey was 8.84 ± 0.16 (SE), and the average abundance was 30.43 ± 1.36. Higher species richness was significantly related to higher values of ACI (GLMM z-value = 3.898, p<0.001, R^2 = 0.72; Figure 6.1a), BIO (z-value = 10.234, p<0.001, R^2 = 0.76; Figure 6.1b) and NDSI (z-value = 3.919, p<0.001, R^2 = 0.23; Figure 6.1c), and lower values of H (z-value = -2.631, p=0.009, R^2 = 0.43; Figure 6.1d). The values of BIO were significantly higher in the morning than in the evening (z-value = 15.000, p<0.001; Figure 6.1b). There were no significant associations between species richness and ADI, nor between total abundance and any of the acoustic indices, and the interactions of species richness and abundance with recording time were not significant (see full model outputs in Supplementary Material S6.2).

6.3.2. *Effects of soundscape on vineyard visitors' experience*

We received 186 (median: 6, range: 1-23 per tour group) questionnaire responses, of which 107 were from the ambient ('off' trials) soundscape tours, and 79 from the enhanced ('on' trials) soundscape tours. Most participants were female (70%) but the distribution of females and males across the two experimental conditions was similar (see Supplementary Material S6.3). An equal number of participants were 18-40 years of age, and 41 and above. Participants who reported higher levels of nature interests in their day-to-day life scored significantly higher in terms of *nature connectedness* (linear model: t-value = 5.559, p-value < 0.001), *tour satisfaction* (t-value = 5.187, p-value = 0.013) and, for participants who were >40 years of age, *vineyard perception* (t=value = 2.690, p-value = 0.008; Supplementary Material S6.3). More generally, older participants (>40 years of age) scored significantly higher in terms of *vineyard perception* (t-value = =2.109, p-value = 0.040).

Under ambient soundscape conditions (‘off’ trials), *nature connectedness, vineyard perception* and *tour satisfaction* scores were all significantly higher at sites with higher ACI (LMM: z-value = 2.143, p-value = 0.032, R^2 = 0.16; z-value = 3.262, p-value = 0.001, R^2 = 0.16; z-value = 2.979, p-value= 0.003, R^2 = 0.16, respectively) and BIO values (z-value = 2.268, p-value = 0.023, R^2 = 0.16; z-value = 3.405, p-value<0.001, R^2 = 0.16; z-value = 3.050, p-value= 0.002, R^2 = 0.18, respectively), and with lower H values (z-value = -2.333, p-value = 0.020, R^2 = 0.17; z-value = -3.477, p-value<0.001, R^2 = 0.16; z-value = -3.090, p-value = 0.002, R^2 = 0.17, respectively; Figure 6.2). *Vineyard perception* and *tour satisfaction* scores were also significantly higher at sites with lower ADI values (z-value = -2.854, p-value = 0.004, R^2 = 0.15; z-value = -2.748, p-value = 0.006, R^2 = 0.18 respectively; Figure 6.2). There were no significant relationships between participants’ scores and NDSI values (Figure 6.2, Supplementary Material S6.4).

Participants who experienced the enhanced soundscape reported a significantly higher number of bird species heard during their tours compared to participants who experienced the ambient soundscape at the same site (‘on’ trials: 3.60 ± 0.22 SE; ‘off’: 2.40 ± 0.18; paired t-test: t(120.8) = 3.604, p<0.001). Scores for *nature connectedness* and *vineyard perception* were significantly higher under soundscape enhancement (‘on’: 3.61 ± 0.08 and ‘off’: 3.37 ± 0.07; z-value = 2.02, p = 0.043, R^2 = 0.20; ‘on’: 3.76 ± 0.08 and ‘off’: 3.55 ± 0.07; GLMM: z-value = 1.99, p-value = 0.047, R^2 = 0.17, respectively; Figure 6.3), but there was no significant effect on participants’ *tour satisfaction* scores (‘on’: 4.17 ± 0.07 and ‘off’: 4.09 ± 0.07; z-value = 0.61, p-value > 0.05; Supplementary Material S6.4).

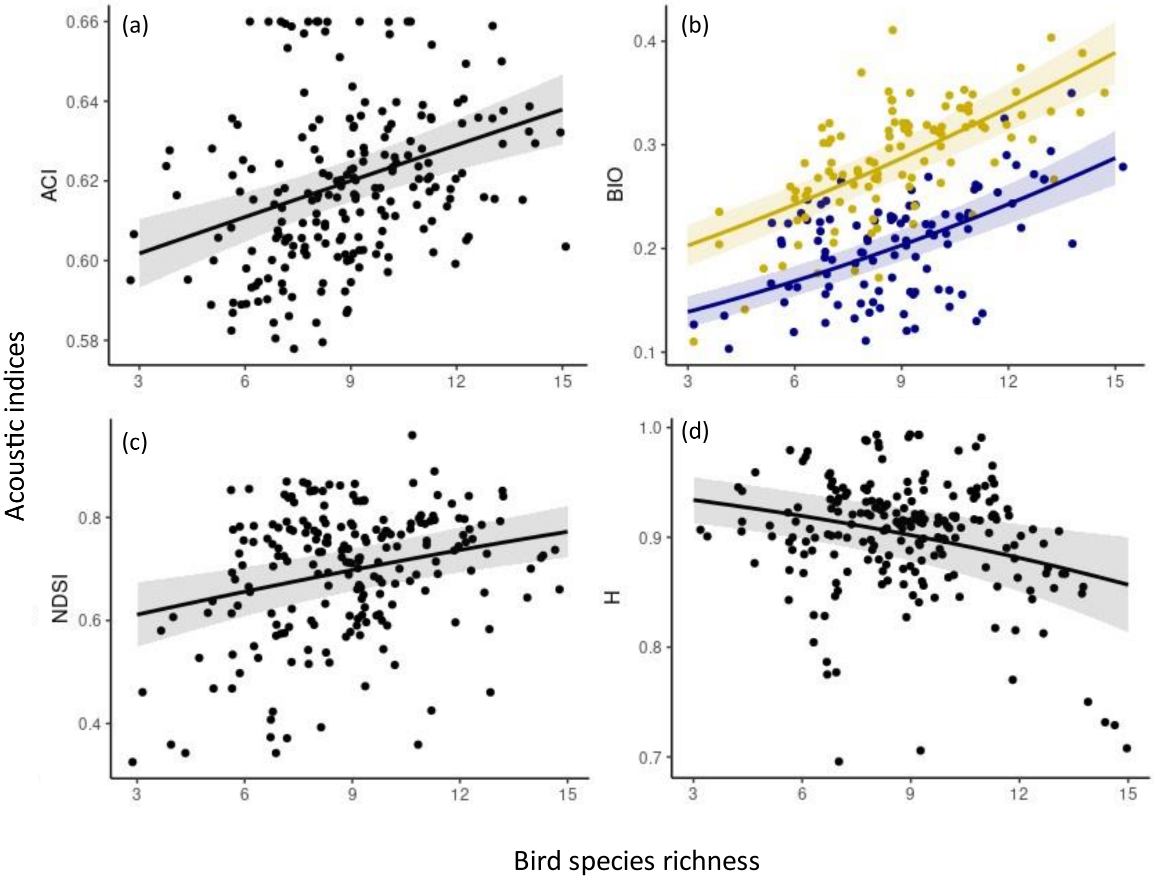
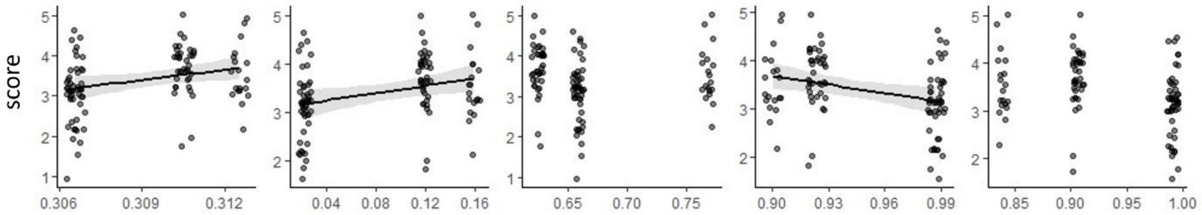
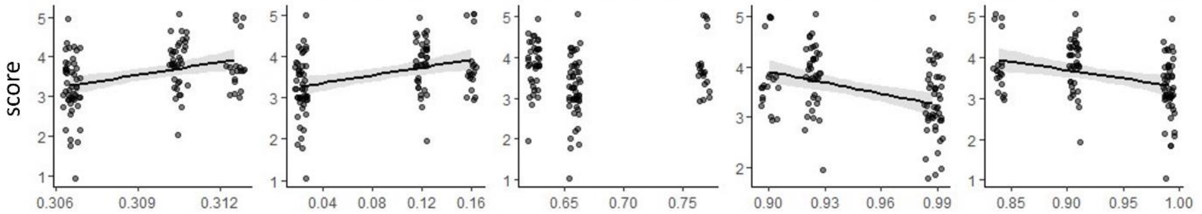


Figure 6.1. Significant relationships between standardised acoustic indices **(a):** ACI: Acoustic Complexity Index; **(b):** BIO: Bioacoustic Index; **(c)**: NDSI: Normalised Difference Soundscape Index; and **(d)**: H: Acoustic Entropy Index, and bird species richness across 21 English vineyards (raw values are jittered for clarity). The line presents model predicted values with 95% confidence intervals (shading) from generalised linear mixed models, and the points indicate raw standardised acoustic index values (n=208 samples). In **(b),** yellow = 'morning' recordings, and blue = 'evening' recordings, as these were significantly different from each other (see Supplementary Material S6.2).

(a) Nature connectedness



(b) Vineyard Perception



(c) Tour satisfaction

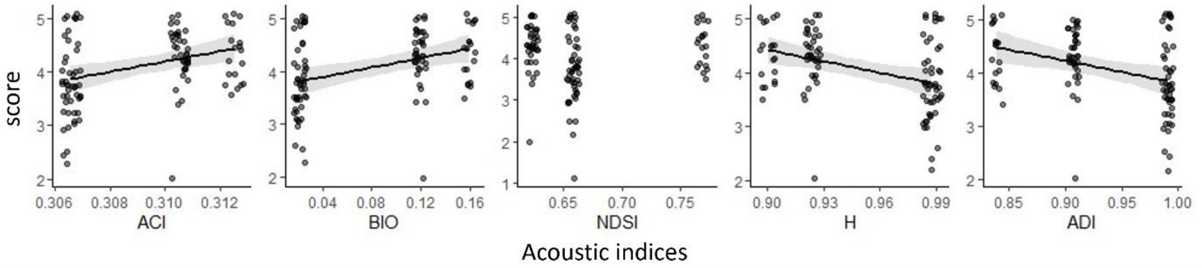


Figure 6.2. The relationship between five standardised acoustic indices (ACI: Acoustic Complexity Index; BIO: Bioacoustic Index; NDSI: Normalised Difference Soundscape Index; H: Acoustic Entropy Index; ADI: Acoustic Diversity Index) as measured in the flowering season, and participants' experience of vineyard tours in relation to the vineyards' ambient soundscape, as measured in three scores: (**a**) *nature connectedness,* (**b**) *vineyard perception* and (**c**) *tour satisfaction,* where higher values indicate more positive experiences. The line presents model predicted values with 95% confidence intervals (shading) from linear mixed models, and the jittered points indicate raw scores at each of three different vineyards (n=107).

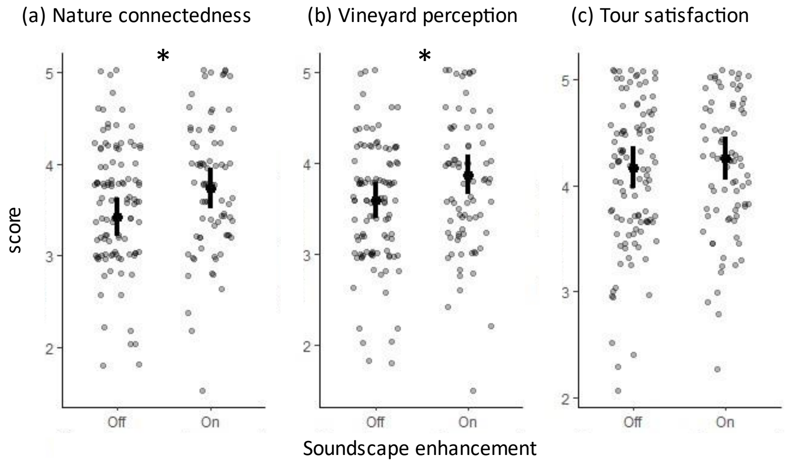


Figure 6.3. Black circle with bars shows the average scores with standard error for (**a**) *nature connectedness,* (**b**) *vineyard perception* and (**c**) *tour satisfaction*, which measured participants' experience in relation to the vineyards' soundscape, and where higher scores indicate more positive experiences. The soundscape was ambient in the 'off' condition and enhanced using birdsong playback in the 'on' condition. Jittered points indicate raw scores for the two conditions (n=107 for 'off' and n=79 for 'on'). Significant differences between conditions, as tested through linear mixed models, are indicated with * which represents significance at $p<0.05$ level.

6.4. Discussion

We demonstrate the link between bird species richness and soundscape complexity and volume in UK vineyards and show that these soundscape characteristics have positive effects on vineyard visitors' experience, increasing levels of reported *nature connectedness*, *vineyard perception*, and *tour satisfaction*. Our experimental soundscape enhancement demonstrates the direct contribution of the aural modality to our experiences of nature.

6.4.1. Relationship between bird diversity and acoustic indices

Sites and sampling seasons with higher avian species richness had more diverse and louder soundscapes. This closely mirrors patterns reported in similar studies from both tropical (Bradfer-Lawrence *et al.*, 2019) and temperate systems (Eldridge *et al.*, 2018), with larger bird communities resulting in a higher diversity of frequency bands being occupied and greater temporal variation in the sound energy across the soundscape. Bird activity is greatest in early mornings, so dawn soundscapes are expected to be louder and more diverse (Dröge *et al.*, 2021). In support of this, we found higher BIO values in the mornings, which indicates higher amplitude of sounds (Boelman *et al.*, 2007; Fuller *et al.*, 2015; Pieretti *et al.*, 2011). One acoustic metric, ADI, which measures the evenness of soundscapes, did not predict species richness well. This could be because the relationship between soundscape evenness and species richness is not linear, with both quiet soundscapes with little song, and diverse soundscapes with continuous song, being characterised by high evenness; some studies have reported a weak decline in evenness with greater richness (e.g. Bradfer-Lawrence *et al.*, 2019; Eldridge *et al.*, 2018), with others reporting evenness to increase with species richness (e.g. Fuller *et al.*, 2015; Mammides *et al.*, 2017).

Contrary to other research (Boelman *et al.*, 2007; Bradfer-Lawrence *et al.*, 2019), we found no relationship between acoustic indices and bird abundance. This could be because abundance is highly variable across the sampling seasons (Zielonka *et al.*, 2023, Chapter 3), and holds a comparatively weaker relationship with acoustic indices than species richness (Bradfer-Lawrence *et al.*, 2020). Additionally, the species likely contributing most to our soundscapes are territorial and have small communities, whilst the most abundant species, such as Woodpigeons *Columba palumbus* and Rooks *Corvus frugilegus*, have simple calls and are less likely to contribute to soundscapes. The difference may also arise from methodological differences between our and aforementioned studies, which compared acoustic indices with diversity data collected at the same point in time, whilst we related bird diversity from a single point count to acoustic index values calculated across recording periods stretching weeks. Acoustic index values can change rapidly over short periods of time, as animals move in relation to the recorders, whilst species richness stays more stable (Alcocer *et al.*, 2022; Bradfer-Lawrence *et al.*, 2023). Taken together, this shows that to fully describe soundscapes and detect the drivers of their variation, studies should use an ensemble of metrics and perform monitoring at scales meaningful to the question.

6.4.2. Effects of soundscape on vineyard visitors' experience

We found a clear link between soundscape characteristics and vineyard visitors' experience. The increase in reported *nature connectedness, vineyard perception* and *tour satisfaction* with BIO indicate a positive association with soundscape volume, whilst the differences in responses with varying ACI, H and ADI values indicate a positive effect of soundscape complexity. This aligns with earlier findings that showed bird diversity and birdsong have a positive effect on life satisfaction and wellbeing (Dallimer *et al.*, 2012; Hammoud *et al.*, 2022; Methorst *et al.*, 2021), support restoration from stress and fatigue (Ratcliffe *et al.*, 2013), and alleviate feelings of anxiety and paranoia (Stobbe *et al.*, 2022). Unlike Fisher *et al.* (2021), we did not find this specific relationship being reflected in NDSI values, likely because Fisher *et al.* made comparison between dense urban and green spaces, reflecting a stronger gradient of anthrophony compared to that present across our sites.

Soundscape enhancement had a significantly positive effect on both *nature connectedness* and *vineyard perception,* crucially highlighting the direct contribution of the aural modality on visitors' experiences. Whilst similar effects of soundscape enhancement have been demonstrated on hiking trials (Ferraro *et al.*, 2020), the patterns were not replicated under a laboratory setting that isolated the effect of aural stimuli (Douglas and Evans, 2022), which raised questions as to whether sounds and sights associated with nature interact to deliver wellbeing benefits. Indeed, the results from the 'off' trials could arise because sound is a proxy for other habitat characteristics that directly benefit wellbeing, such as canopy cover or the perceived beauty of green spaces (Joye and Bolderdijk, 2015; Zhang *et al.*, 2022), but the experimental soundscape enhancement ensured only aural characteristics changed, with additional modalities for nature engagement kept stable. Introducing additional bird song on top of the ambient soundscape increased its complexity and volume, and the resultant increases in *nature connectedness* and *vineyard perception* reinforce the specific contribution of birdsong to perceptions of biodiversity and delivery of benefits from nature engagement (Buckley, 2022; Douglas and Evans, 2022; Ferraro *et al.*, 2020; Hammoud *et al.*, 2022; Smalley *et al.*, 2022; Stobbe *et al.*, 2022). Importantly, we found the effect of soundscape enhancement to be supported even in sites with higher baseline ACI, ADI, H and BIO values, which emphasises that there are opportunities to further improve natural soundscapes through vineyard conservation practices that increase bird diversity (e.g. Zielonka *et al.*, 2023, Chapter 4). Our soundscape enhancement did not result in an improvement of *tour satisfaction,* and we hypothesise that the relative influence of other factors, such as the tour guide's demeanour, is likely greater on this aspect of visitors' experience.

At the individual level, the degree to which soundscapes alleviate mental fatigue and improve wellbeing can be influenced by a number of factors (Ratcliffe *et al.*, 2013). In line with previous research (Capaldi *et al.*, 2014), we found that the level of participants' nature interests correlated positively with their scores for *nature connectedness, vineyard perception* and *tour satisfaction*. This could be because individual's attitudes towards nature affect their ability to subconsciously notice, natural sounds, such as birdsong (Soga and Gaston, 2016) and report increased wellbeing (Capaldi *et al.*, 2014). This could also be because familiar sounds are more restorative (Ednie and Gale, 2021; Ratcliffe, 2021), perhaps by triggering positive memories (Smalley *et al.*, 2022). As levels of nature connectedness decline, particularly among the younger generation and those living in cities (Kesebir and Kesebir, 2017; Schweizer *et al.*, 2007; Soga and Gaston, 2016), it would be interesting to research whether different groups of people benefit more or less from exposure to soundscapes. We enhanced our soundscapes through the addition of five species and further investigation could also identify whether these trends continue indefinitely, or level off, whilst also considering the interaction of bird song with other sources of biophony and geophony that have been shown to elicit feelings of connectedness (Ednie and Gale, 2021; Hallmann *et al.*, 2017; Sharif *et al.*, 2023).

6.5. Synthesis and applications

As biodiversity losses continue, particularly in agricultural areas (Rigal *et al.*, 2023), and people's access to greenspaces becomes more limited (Buxton *et al.*, 2021; Morris *et al.*, 2011), creating new and accessible opportunities to experience natural soundscapes, whilst also delivering biodiversity conservation, is vital. Given the importance of the tourism industry within viticulture (Sussex Modern, 2023), and given the link between soundscape complexity and visitors' perception, it is of particular interest to vineyard managers to create complex natural soundscapes. At one extreme, this could potentially be achieved through artificial birdsong playback. However, this would require significant investment in technology and maintenance and would come without any conservation benefit. Furthermore, research has demonstrated that real-life experiences of nature lead to greater improvements in our mood and wellbeing compared to virtual or laboratory-based settings (Browning *et al.*, 2020; Douglas and Evans, 2022). Instead, the ambition should be to increase bird richness in vineyards through, for example, diversification of habitats and ground cover, reduced chemical use (Barbaro *et al.*, 2022;

Zielonka *et al.*, 2023), and the provision of nest boxes (Caprio and Rolando, 2017; Jedlicka *et al.*, 2011). There could be potential monetary gains associated with investing in bird conservation measures in vineyards. We found *tour satisfaction*, which included a measure of how likely visitors were to recommend the vineyard tour, to be higher at sites with more complex soundscapes, which supports earlier trends between positive soundscape perception and increased tourism loyalty (Jiang and Yan, 2022). Studies have also shown that natural sounds alter consumer behaviour and affect food choices and sales (Kontukoski, 2018; Peng-Li *et al.*, 2022), and so, we hypothesise that more positive experiences of nature delivered through complex soundscapes could translate both to increased participation in vineyard tours and increased wine sales in vineyards, or similar businesses, leading to a win-win-win for biodiversity conservation, visitors' wellbeing and business prosperity.

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Chapter 6 Supplementary Materials

S6.1. Vineyard visitor questionnaire, participant information and debrief sheets

Questionnaire ID: XXX

Time of tour:		Date:		Group size:	

How long will this take? It should only take a few minutes to complete.
Who is running this survey? It is being conducted by a University of East Anglia master's student, Victoria Tubman, as part of their dissertation research.
What is the aim of this questionnaire? The aim is to investigate people's perception of the vineyard landscape and their connectedness to nature and wellbeing. The results of this survey will be used for UEA's research purposes and may be shared in presentations and in journals.
Is your participation necessary? Your participation is very important to us, and we value the information you provide, but participation in this survey is completely voluntary.

Do you agree to take part in this survey? YES / NO
(please circle – this is a vital question)

Gender identity	
Female	
Male	
Other	
Prefer not to say	

Age category:	Please tick
18-29	
30-39	
40-49	
50-59	
60-69	
70+	
Prefer not to say	

Please can you place an **X** under the level of agreement for each statement.

1= Strongly disagree **2**= Disagree **3**= Neutral **4**= Agree **5** =Strongly agree

Interests:	1	2	3	4	5
I am an urban-oriented person, finding pleasure in street life, shopping, and amusements of the city?					
I am a nature-oriented person, finding pleasure in the sea, woods, and nature?					
Being out in nature is a great stress reducer for me.					
I often buy products that are labelled organic.					
I often buy products buy fair trade items					
Supporting environmentally friendly or nature organisations (such as the RSPB or a local wildlife trust) is important to me.					
I participate in nature-related activities (such as bird watching or nature walks)					

Please can you place an **X** under the level of agreement that reflects your current mood and perception for each statement.

1= Strongly disagree **2**= Disagree **3**= Neutral **4**= Agree **5** =Strongly agree

Questions:	1	2	3	4	5
Spending outside on this vineyard tour makes me feel more connected to nature					
The sounds I heard on the vineyard tour today were appealing.					
The sounds I heard seem to fit together quite naturally within the vineyard landscape					
Along the vineyard tour route my attention was drawn to many interesting sounds					
The sounds made me want to linger along the tour route.					
Nature sounds are an important source of information for me to assess if it is biodiverse (has many different species).					
I feel more optimistic during and immediately after this vineyard tour					
I feel relaxed during and immediately after this vineyard tour					
Hearing the natural sounds at the vineyard today made me feel free from work, routine, and responsibilities					
The natural sounds on the tour today were overwhelming and hindered my experience					
It was important for me to listen to the bird song on the vineyard tour					
Sounds of nature are important for my perception of bird species in the area					
I was engrossed by the sounds I heard along the vineyard tour					
The sounds I heard on the tour route all belonged there.					
Based on today's vineyard tour, and experience of the acoustic environment, I would recommend this experience to others.					

	Approx. Number:
Approximately how many different bird species would you say you heard along todays vineyard tour?	

Should you wish to remove your response from the research, please email *Researcher's Email* quoting the ID number at the top of this questionnaire.

If you have any concerns, please get in touch with the University of East Anglia's Head of the School of Biological Sciences (*Name and Email address*).

Thank you for completing this form – it is greatly appreciated!

Debrief sheet for 'The impact of vineyard management on pollinator diversity, and the impact of biodiversity on visitors' wellbeing'

Thank you for your time, during this tour you will have experienced either five extra bird species songs being played through speakers placed around the vineyard or the natural sounds of the vineyard. Current research is finding support for the link between mental health with nature experiences, and that where this experience is enhanced that perceived wellbeing increases further. Ultimately, providing an argument that biodiversity plays an important part in natural environments and their subsequent restorative effects. Past research by Ferraro et al (2020) - '*The phantom chorus: birdsong boosts human well-being in protected areas*', showed that where bird song had been played along nature trails, that individuals had reported higher wellbeing.
No research to date has investigated the effect of bird song soundscapes within vineyards on wellbeing and I hope to use the conclusions from this survey to further increase information in this developing area of knowledge. It may also provide evidence that protecting biodiversity can increase the wellbeing of those experiencing the environment.

If you would like to withdraw any information provided, please email v.tubman@uea.ac.uk quoting the ID number at the top of your questionnaire.

If you have any concerns, please get in touch with the Head of University of East Anglia's School of Biological Sciences (*Name and Email address*).

S6.2. Model outputs – acoustic indices in relation to bird biodiversity

Table S6.2. Model estimates (with 95% confidence intervals) from generalised linear mixed models, relating five acoustic indices (ACI: Acoustic Complexity Index; ADI: Acoustic Diversity Index; H: Acoustic Entropy Index; BIO: Biophony Index; NDSI: Normalised Difference Soundscape Index) as response variables to bird species richness and abundance. Models also included an interaction term between bird species richness and abundance and the recording time and were fitted with the recording period (6 levels) and Audio ID nested in site (32 Audio IDs, nested in 21 sites) as random effects. The model intercept included ‘evening’ recording time as the reference level. See 6.2. for details of data collection. Significant relationships are highlighted in blue.

Response	Predictor variable	Estimate	Std. Error	z-value	p-value	AIC	R2
ACI	Intercept	0.365 (0.306 - 0.424)	0.030	12.123	<0.001	-1073	0.72
	Bird species richness	0.013 (0.006 - 0.019)	0.003	3.898	<0.001		
	Bird Abundance	-0.0002 (-0.001 - 0.001)	0.0004	-0.567	0.571		
	Recording time (morning)	0.074 (-0.002 - 0.151)	0.039	1.897	0.058		
	Bird species richness * Recording time (morning)	-0.002 (-0.010 - 0.007)	0.004	-0.347	0.729		
	Bird Abundance * Recording time (morning)	-0.001 (-0.002 - 0.0003)	0.001	-1.383	0.167		
ADI	Intercept	1.946 (1.256 - 2.636)	0.352	5.529	<0.001	-509	0.12
	Bird species richness	0.010 (-0.061 - 0.081)	0.036	0.269	0.742		
	Bird Abundance	-0.001 (-0.009 - 0.007)	0.004	-0.328	0.771		
	Recording time: morning	0.581 (-0.244 - 1.407)	0.421	1.380	0.168		
	Bird species richness * Recording time (morning)	-0.032 (-0.127 - 0.063)	0.049	0.048	0.515		
	Bird Abundance * Recording time (morning)	0.001 (-0.010 - 0.012)	0.006	0.132	0.894		
Response Variable	Predictor variable	Estimate	Std. Error	z-value	p-value	AIC	R2
H	Intercept (evening)	2.887 (2.411 - 3.364)	0.194	11.875	<0.001	-658.4	0.43
	Bird species richness	-0.066 (-0.116 - -0.017)	0.019	-2.631	0.009		
	Bird Abundance	-0.002 (-0.008 - 0.004)	0.002	-0.716	0.474		
	Recording time (morning)	-0.013 (-0.634 - 0.609)	0.073	-0.039	0.968		
	Bird species richness * Recording time (morning)	-0.003 (-0.071 - 0.065)	0.029	-0.084	0.933		
	Bird Abundance * Recording time (morning)	0.002 (-0.006 - 0.010)	0.003	0.507	0.612		
BIO	Intercept (evening)	-1.992 (-2.185 - -1.798)	0.074	-27.740	<0.001		0.76

	Bird species richness	0.068 (0.047 - 0.089)	0.007	10.234	<0.001	-725.6	
	Bird Abundance	-0.0002 (-0.003 - 0.002)	0.001	0.374	0.709		
	Recording time: morning	0.403 (0.165 - 0.642)	0.03	15	<0.001		
	Bird species richness * Recording time (morning)	0.005 (-0.022 - 0.032)	0.029	0.756	0.450		
	Bird Abundance * Recording time (morning)	0.001 (-0.002 - 0.004)	0.003	1.262	0.207		
NDSI	Intercept (evening)	0.400 (-0.011 - 0.810)	0.172	1.395	0.163	-343.5	0.23
	Bird species richness	0.064 (0.012 - 0.116)	0.016	3.919	<0.001		
	Bird Abundance	-0.002 (-0.007 - 0.003)	0.002	0.169	0.866		
	Recording time (morning)	-0.292 (-0.784 - 0.200)	0.061	0.360	0.719		
	Bird species richness * Recording time (morning)	0.022 (-0.035 - 0.079)	0.029	0.756	0.450		
	Bird Abundance * Recording time (morning)	0.004 (-0.002 - 0.011)	0.003	1.262	0.207		

S6.3. Description of participants' demographic and interest in nature variables, and their effect on the participants' experience of the vineyard soundscape

Altogether, 186 participants completed the questionnaire, which included 131 females and 50 males, and 91 participants were between 19 and 40 years of age, whilst 90 were above 40 (five out of the participants did not provide information on their gender or age, Figure S6.3.1).

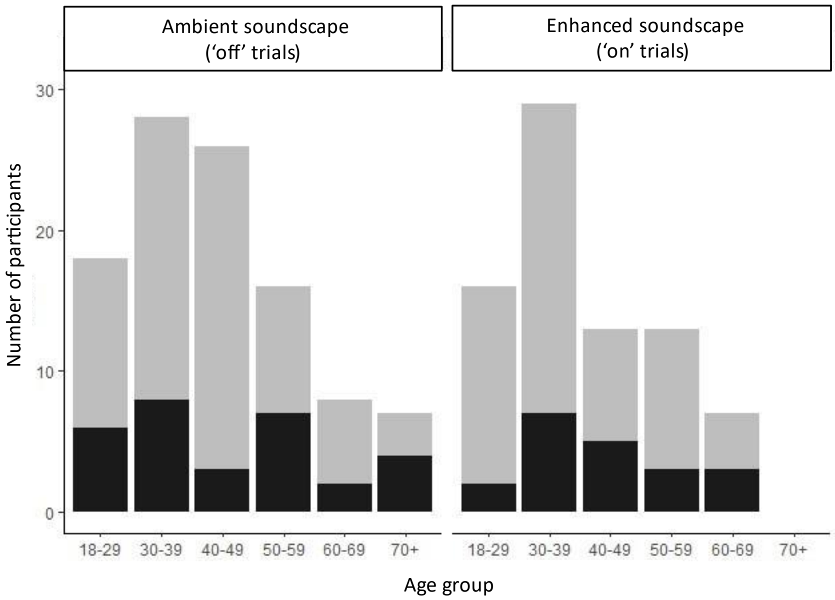


Figure S6.3.1. Distribution of responses to our questionnaire based on participants' gender (grey: female, black: male), age and whether the participants experienced ambient or enhanced soundscape during their vineyard tour. Total number of participants was 186, but five participants did not provide age or gender information.

Within the questionnaire, we measured participants' interests in nature by seven Likert-scale questions (see Supplementary material S6.1) and averaged the participants' responses in an aggregate *nature interest* score. We tested the reliability of the seven questions that measured *nature interest*, and based on all seven questions the reliability was quite low (Cronbach's Alpha: α = 0.621, 95% CI 0.554-0.689). We removed one question *("I am an urban-oriented person, finding pleasure in street life, shopping, and amusements of the city"*), which sufficiently improved the reliability of this measure (α = 0.721, 95% CI 0.645 – 0.779).

To check whether participants' gender, age (two groups: <40 and >40) or *nature interests* affected their experience of the vineyard's soundscape, we related these variables to the three scores (*nature connectedness, vineyard perception* and *tour satisfaction*), which we fitted as response variables in linear models with gaussian error distribution. We also included an interaction term between the *nature interests* score and participants' gender and age. We found that higher scores for *nature connectedness* and *tour satisfaction* were significantly related to the participants scoring higher on *nature interests* (Table S6.3.1, Figure S6.3.2a-b). Vineyard perception was significantly higher in older participants (Table S6.3.1, Figure S6.3.2c), whilst a significant positive effect of the interaction between *nature interests* scores and age group was supported (Table S6.3.1, Figure S.6.3.2d).

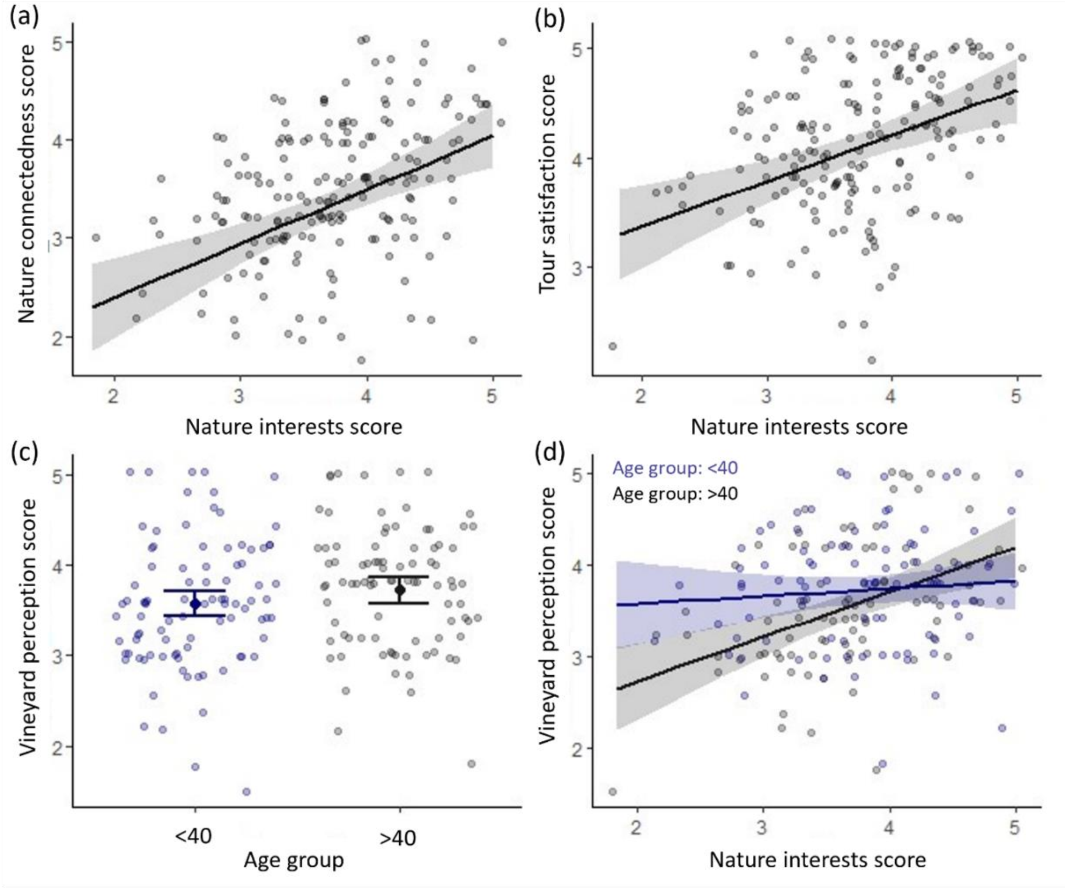


Figure S6.3.2. Model predicted (with 95% confidence intervals) significant relationships between scores that quantified responders' experience of vineyard tours in relation to the vineyards' soundscapes (*nature connectedness, vineyard perception* and *tour satisfaction)* to responders' (n=181) level of nature interest (*nature interest* score: **a, b, d**) and age (below 40 years of age - blue; above 40 years of age – black; **c** and **d**). Dots indicate raw scores from the questionnaires.

Table S6.3.1. Model estimates (with 95% confidence intervals) from linear models relating the three scores that quantified visitors’ experience of vineyard tours in relation to the vineyards’ soundscapes (*nature connectedness, vineyard perception* and *tour satisfaction*) to responders’ (n=181) gender, age and level of nature interest (*nature interest* score). Information on visitors’ experience of the vineyard soundscape was collected through a questionnaire across 3 vineyards that ran tours (see S6.1 for details). Significant relationships are highlighted in blue.

Response variable	Predictor	Estimate (95% CI)	Std. Error	t-value	p-value
Nature connectedness	Intercept (Age >40 / Gender: F)	2.09 (1.50 – 2.68)	0.300	6.976	<0.001
	Age (<40)	-0.79 (-1.89 – 0.31)	0.094	-1.417	0.158
	Gender (M)	-0.003 (-0.21 – 0.21)	0.106	-0.025	0.980
	Nature interest score	0.42 (0.27 – 0.57)	0.075	5.559	<0.001
	Nature interest score * Age (<40)	0.13 (-0.16 – 0.42)	0.148	0.889	0.375
	Nature interest score * Gender (M)	-0.28 (-0.62 – 0.07)	0.174	-1.599	0.111
Vineyard perception	Intercept (Age >40 / Gender: F)	3.41 (2.52 – 4.31)	0.452	7.555	<0.001
	Age (<40)	-1.67 (-2.80 - -0.54)	0.573	-2.109	0.040
	Gender (M)	-0.57 (-1.86 – 0.73)	0.656	-0.865	0.482
	Nature interest score	0.08 (-0.15 – 0.31)	0.117	0.704	0.388
	Nature interest score * Age (<40)	0.41 (0.11 – 0.71)	0.152	2.690	0.008
	Nature interest score * Gender (M)	0.19 (-0.16 – 0.54)	0.179	1.056	0.292
Tour satisfaction	Intercept (Age >40 / Gender: F)	2.86 (2.31 – 3.41)	0.279	10.253	<0.001
	Age (<40)	-0.13 (-0.30 – 0.05)	0.088	-1.460	0.146
	Gender (M)	-0.04 (-0.24 – 0.15)	0.099	-0.446	0.656
	Nature interest score	0.27 (0.06 – 0.48)	0.070	5.187	0.013
	Nature interest score * Age (<40)	0.15 (-012 – 0.42)	0.138	1.091	0.277
	Nature interest score * Gender (M)	0.09 (-0.23 – 0.41)	0.164	0.549	0.584

S6.4. Model outputs – vineyard visitors’ experience in relation to soundscape

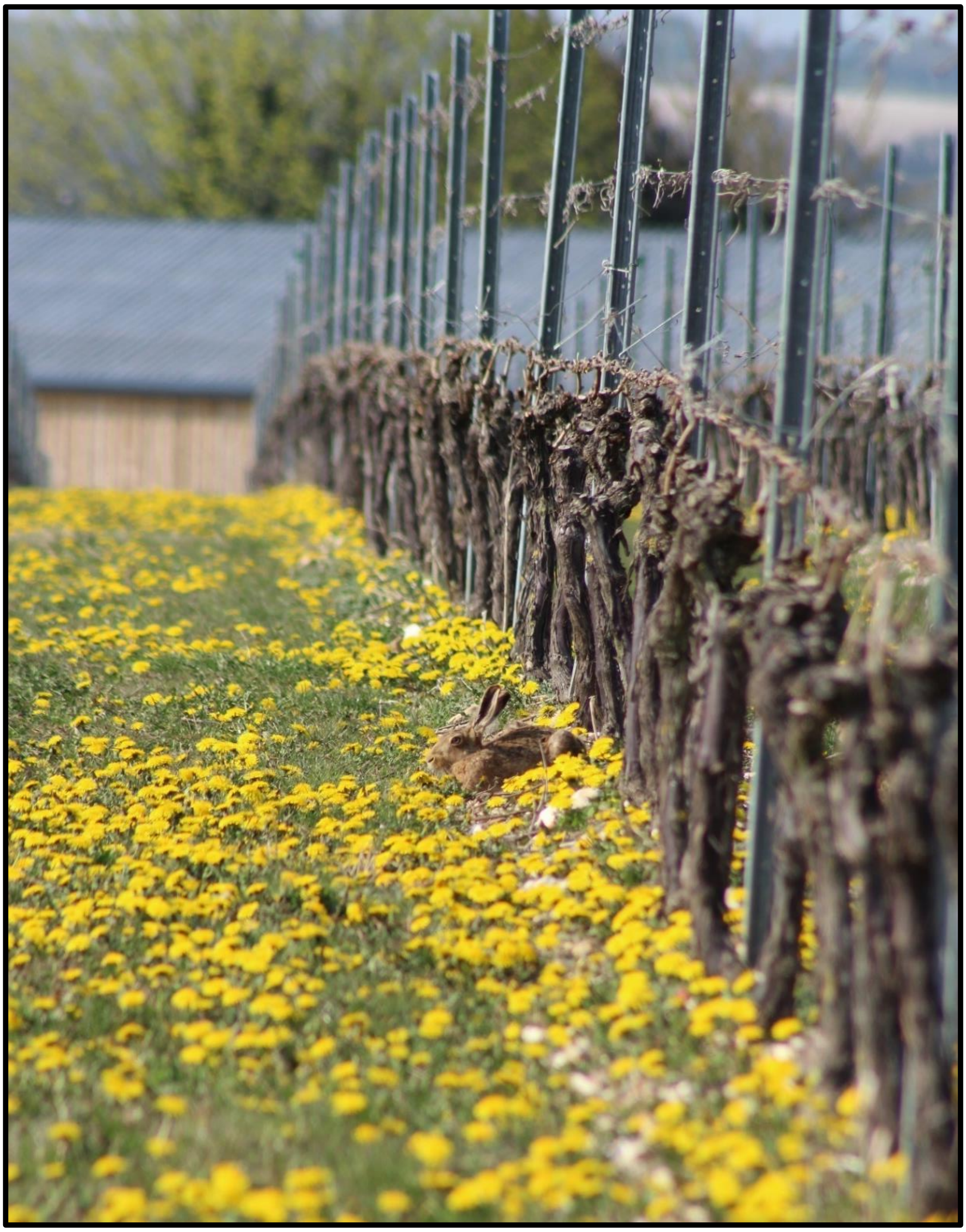
Table S6.4.1. Model estimates (with 95% confidence intervals) from linear mixed models, relating three scores that quantified participants’ experience of vineyard tours in relation to the vineyards’ ambient soundscape (nature connectedness, vineyard perception and tour satisfaction) to five acoustic indices (ACI: Acoustic Complexity Index; ADI: Acoustic Diversity Index; H: Acoustic Entropy Index; BIO: Biophony Index; NDSI: Normalised Difference Soundscape Index), which characterised the vineyards’ soundscape. Models included the random effect of tour group ID (24 levels) nested in site (3 levels). See 6.2. for details of data collection. Significant relationships are highlighted in blue.

	Predictors	Estimate (95% CI)	Std. Error	z-value	p-value	AIC	R2
Nature connectedness score	Intercept	-2.91 (-4.71 - 0.19)	12.3	-1.863	0.062	230.7	0.16
	ACI	8.52 (0.73 - 16.30)	3.97	2.143	0.032		
	Intercept	6.29 (3.21 - 9.36)	1.57	4.001	<0.001	231.5	0.15
	ADI	-3.08 (-6.41 - 0.26)	1.701	-1.81	0.07		
	Intercept	9.04 (4.33 - 13.75)	2.402	3.763	<0.001	230.2	0.17
	H	-5.94 (-10.93 - -0.95)	2.547	-2.333	0.02		
	Intercept	3.10 (2.75 - 3.44)	0.18	17.47	<0.001	231.1	0.16
	BIO	3.77 (0.51 - 7.03)	1.67	2.268	0.023		
	Intercept	4.05 (1.45 - 6.65)	1.327	3.051	0.002	234	0.13
	NDSI	-0.89 (-4.76 - 3.00)	1.979	-0.446	0.655		
Tour satisfaction	Intercept	-2.87 (-5.01 - -0.721	1.11	-2.603	0.009	228.6	0.16
	ACI	10.56 (3.61 - 17.51)	3.55	2.979	0.003		
	Intercept	7.97 (5.22 - 10.71)	1.4	5.688	<0.001	229.2	0.18
	ADI	-4.16 (-7.12 - -1.19)	1.512	-2.748	0.006		
	Intercept	10.78 (6.55 - 15.01)	2.158	4.995	<0.001	227.2	0.17
	H	-7.06 (-11.54 - -2.58)	2.285	-3.09	0.002		
	Intercept	3.71 (3.40 - 4.02)	0.158	23.54	<0.001	230.1	0.18
	BIO	4.54 (1.63 - 7.46)	1.488	3.05	0.002		
	Intercept	3.39 (0.81 - 5.96)	1.314	2.576	0.01	234.4	0.14
	NDSI	1.15 (-2.70 - 5.00)	1.962	0.586	0.558		
Vineyard perception	Intercept	-2.98 (-5.00 - -0.98)	1.02	-2.913	0.004	231	0.16
	ACI	10.80 (4.31 - 17.29)	3.31	3.262	0.001		
	Intercept	7.41 (4.78 - 10.04)	1.342	5.52	<0.001	232.2	0.15
	ADI	-4.13 (-6.96 - -1.29)	1.446	-2.854	0.004		
	Intercept	10.50 (6.59 - 14.40)	1.993	5.266	<0.001	230.4	0.16
	H	-7.32 (-11.45 - -3.19)	2.106	-3.477	<0.001		
	Intercept	3.17 (2.89 - 3.44)	0.141	22.389	<0.001	231.1	0.16
	BIO	4.69 (1.99 - 7.39)	1.377	3.405	<0.001		
	Intercept	3.49 (0.94 - 6.05)	1.303	2.682	0.007	237.7	0.14
	NDSI	0.18 (-3.64 - 3.99)	1.944	0.09	0.928		

Table S6.4.2. Model estimates (with 95% confidence intervals) from linear mixed models, relating three scores that quantified participants’ experience of vineyard tours in relation to the vineyards’ soundscape (nature connectedness, vineyard perception and tour satisfaction) to whether the vineyard soundscape was experimentally enhanced. In the ‘off’ trials, we measured the participants’ experience of the ambient soundscape (n=107 responses), whilst in the ‘on’ trials, the soundscape was enhanced with a playback of a constructed bird chorus (n=79). Trials took place across 24 tour groups across three vineyards. Models included the random effect of tour group ID (24 levels) nested in site (3 levels). Significant relationships are highlighted in blue.

Response variable	Predictors	Estimate (95% CI)	Std. Error	z-value	p-value	AIC	R2
Nature connectedness	Intercept (off trials)	3.42 (3.21 - 3.63)	0.107	31.97	<0.001	387.1	0.20
	Soundscape enhancement (on trials)	0.31 (0.01 - 0.61)	0.152	2.02	0.043		
Tour satisfaction	Intercept (off trials)	4.17 (3.98 - 4.37)	0.100	42.01	<0.001	358.3	0.15
	Soundscape enhancement (on trials)	0.08 (-0.19 - 0.36)	0.138	0.61	0.524		
Vineyard perception	Intercept (off trials)	3.59 (3.40 - 3.79)	0.100	35.84	<0.001	385.0	0.17
	Soundscape enhancement (on trials)	0.28 (0.004 - 0.56)	0.143	1.99	0.047		

Chapter 7: General discussion



© Natalia Zielonka, European hare, *Lepus europaeus,* at an English vineyard, Hampshire

Natalia B. Zielonka

7.1. Summary of thesis' findings

Almost 40% of world's ice-free land is dedicated to agriculture, making it the largest land-use (Ellis & Ramankutty 2008), and agricultural expansion and intensification have had profound detrimental effects on world's biodiversity (Newbold *et al.* 2015, Díaz *et al.* 2019, WWF 2022). Despite considerable research highlighting unsustainable agricultural practices as leading drivers of biodiversity loss (Beyer & Manica 2019, Burns *et al.* 2021, Nicholson *et al.* 2023, Rigal *et al.* 2023), and global efforts to tackle the biodiversity crisis (Mace *et al.* 2018, IPBES 2019), the strength of agriculture-related threats to nature is not decreasing (Tilman *et al.* 2011, Campbell *et al.* 2017, Potapov *et al.* 2022). To address the biodiversity crisis, agricultural systems need to be urgently transformed into *multifunctional landscapes* that deliver benefits for people and nature (Kremen & Merenlender 2018, Leclère *et al.* 2020, WWF 2022). This requires a knowledge base to inform how, where and when, biodiversity could be conserved within, and contribute to the functioning of, high-yielding agricultural landscapes (Bommarco *et al.* 2013, Kremen 2020, Berger *et al.* 2023). This thesis' findings contribute to this knowledge base, and to facilitate the shift towards multifunctional thriving landscapes, I make management and policy recommendations for how biodiversity conservation could be incorporated within perennial fruit farm landscapes of north-eastern Brazil and southern England, and I identify avenues for future research.

7.1.1. Biodiversity responses to fruticultural expansion in the Caatinga

While agricultural expansion has mostly stopped across Europe, the rates of expansion are accelerating across South America where agricultural land is replacing native habitats, home to many endemic species (Dias *et al.* 2016, Salazar *et al.* 2021, Potapov *et al.* 2022). The rise in export-oriented agriculture to meet the growing food demands in high-income countries is often fuelling these expansions (Kastner *et al.* 2021). Here, we undertook the first assessment of bird communities across fruit farms in north-eastern Brazil, providing a small-scale snapshot of how biodiversity might be responding to the recent rise in export fruticulture in the Caatinga biome. We show that **the expansion of fruticulture is having a detrimental effect on bird communities and may be fuelling homogenisation of bird assemblages** (Chapter 2). The fruit farms are simply structured in comparison to the neighbouring Caatinga forest, and they are intensively managed and associated with high levels of disturbance, so it is not surprising that they are characterised by lower bird abundance and diversity. Additionally, we showed that fruit farms are predominantly occupied by generalist species at the loss of more specialist species. From a conservation perspective, the most concerning pattern was the **significantly reduced abundance of some endemic species, whilst also noting high abundance of two non-native species within the fruit farms** (Chapter 2). Continuing agricultural expansion across the Caatinga can therefore be expected to result in homogenisation of avian communities and lead to an overall loss of avian biodiversity, whilst jeopardising the potential for ecological intensification, especially through the decline in insectivorous species, which could be incorporated into farmland management as biological pest control agents (Pejchar *et al.* 2018).

The benefits of retaining semi-natural habitats across agricultural landscapes for bird biodiversity have been widely documented (Ramos *et al.* 2018, Redlich *et al.* 2018, Adorno *et al.* 2021), and to support biodiversity conservation, globally, almost 40% of the world's countries have set minimum area requirements for the conservation or restoration of native vegetation within agricultural landscapes (Garibaldi *et al.* 2021). For example, Brazil's Forest code requires a portion of land to be set aside in native habitats, with the amount varying between regions of Brazil and property size, and is set at 20% outside of 'Legal Amazon' (WWF Brazil 2016), which aligns with the proposal that multifunctional landscapes need 20% of native habitats to deliver multiple ecosystem services benefitting production and human wellbeing more widely (Garibaldi *et al.* 2021). Across our Brazilian fruit farms, we **did not find significant benefits of increasing Caatinga cover, nor of edge density on avian communities** (Chapter 2), and so, we suggest that retention of Caatinga forests across agricultural landscapes *per se* may not harness the expected biodiversity benefits. This could be because many Caatinga species are forest specialists (Araujo & Da Silva 2017), and are unable to adapt to the high-contrast landscapes, which may also limit species spill-over (Boesing *et al.* 2021, Alvarez-Alvarez *et al.* 2022). The relationship between the area of semi-natural habitats and biodiversity is likely context-dependent, whilst most current area-based habitat conservation targets are arbitrary (Berger *et al.* 2023), rather than based on empirical evidence, and I believe that there needs to be a shift towards research considering how much and where semi-natural habitats could be incorporated into such intensive Brazilian fruit-farm landscapes, and if practices that have been shown to work elsewhere, such as retention of forest patches and scattered trees to act as stepping stones (Prevedello *et al.* 2018, Silva *et al.* 2020), could support bird conservation in this system. Alongside this, the proportion of Caatinga under strict legal protection (Teixeira *et al.* 2021), away from agricultural areas, needs to expand to conserve species most reliant on the Caatinga forest, which may not be able to adapt to agricultural production and are not compatible with land-sharing scenarios.

7.1.2. Biodiversity responses to viticulture in the UK

European landscapes have been altered by agriculture and urbanisation for centuries and lack many pristine and expansive patches of semi-natural habitats that have not been altered by human activity (Potapov *et al.* 2022). This means that European agricultural communities are already characterised by a high proportion of generalist species that have been able to adapt to agriculture (Robinson & Sutherland 2002). The key threat to biodiversity across European agricultural landscape is intensification, whilst the increase in novel systems arising from changing climatic suitability that is permitting shifts in crop ranges, of which viticulture in the UK is a prime example (Chapter 1), limits our ability to deploy evidence-informed nature-friendly management practices that support both biodiversity and production. To address this gap, we conducted the first assessment of biodiversity and its contributions to production and human wellbeing across UK vineyards (Paiola *et al.* 2020). We showed that **bird and ground-dwelling**

arthropod biodiversity across English vineyards is not affected by the surrounding habitat structure, and that organic management and accreditation through an industry sustainability scheme do not predict biodiversity benefits reliably or consistently (Chapter 4). Crucially, we also showed that **organically managed vineyards have 36% lower yield than non-organic vineyards** (Chapter 5). By considering finer-scale management practices, we instead **identified agrochemical use and ground vegetation cover management to be the key drivers of biodiversity** (Chapter 4), **with potential impacts for yield** (Chapter 5). Incorporating biodiversity into high-yielding agricultural systems requires the understanding of its net effects on production, and we noted an **influx of grape-eating species to vineyards at harvest which we linked to crop damage and, under certain conditions, to a significantly lower yield** (Chapter 5). Nonetheless, we have also demonstrated that **increasing bird richness can increase the provision of cultural ecosystem services** (Chapter 6), which may benefit wider human wellbeing and business prosperity.

Effects of landscape heterogeneity

Semi-natural habitats across agricultural landscapes make an important contribution to maintaining regional species pools by providing habitat space and key resources to many wild species, and on-farm biodiversity is often the result of invasions from these habitat remnants (Tscharntke *et al.* 2012), which is why semi-natural habitats are usually found to be key drivers of biodiversity within agricultural landscapes, including vineyards (Guyot *et al.* 2017, Steel *et al.* 2017, Muñoz-Sáez *et al.* 2020). English vineyards are unlike many other agricultural systems as they are considerably smaller and more heterogeneous compared to vineyards in other parts of the world, and especially compared to annual cereal or oil crops that are grown as large-scale monocultures. Therefore, despite our study sites spanning a landscape complexity gradient with the semi-natural habitats cover ranging between <1% and 42% (Chapter 3), the differences in habitat heterogeneity characterising the English viticultural industry are likely weaker than those observed elsewhere, as English vineyards maintain a high degree of heterogeneity by retaining linear wooded features, such as hedgerows and tree windbreaks, as well as by having small fields (Chapter 3), which may be facilitating species spill-over, particularly of birds, into and across vine fields. This is reinforced by our finding that **vineyards accredited through the industry sustainability scheme** (SWGB – see Chapter 1) **had significantly larger field sizes and lower bird diversity than non-SWGB vineyards** (Chapter 4). One interpretation of this finding could be that semi-natural habitats are not important for biodiversity conservation across English vineyards, particularly, as **proximity to edge habitats, such as woodlands, increases disservices from birds in the form of crop damage** (Chapter 5). Rather, I propose that the relative importance of on-farm management is simply higher, and that the current management of English vineyards, which maintains heterogeneity, could be beneficial for wider biodiversity.

Effects of management

The goal of organic management is to reduce the environmental impact of farming, and its uptake is advocated as means to reconcile agriculture with biodiversity conservation (e.g. European Commission 2023). However, a concern about the widespread and increasing uptake of organic agriculture is the potential of reduced agricultural yields due to land being taken out of production and turned into semi-natural habitats or farmed less intensively, which could fuel further agricultural expansion to meet the demands for agricultural goods. Our results suggest that **organic management is not a sustainable approach for English viticulture, as we found organic vineyards to have significantly lower yields** (Chapter 5, supporting findings from de Ponti *et al.* 2012, Seufert *et al.* 2012, de la Cruz *et al.* 2023), **but without consistent biodiversity benefits** (Chapter 4, contradicting Schneider *et al.* 2014, Tuck *et al.* 2014, Smith *et al.* 2020). In agreement with earlier research (e.g. Rusch *et al.* 2015, Froidevaux *et al.* 2017, Ostandie *et al.* 2021), we found a positive effect of organic management for arthropods but not for birds (Chapter 4). Birds and arthropods are influenced by processes that operate at different scales, with arthropods being more strongly affected by small-scale patches and their management (Riva & Fahrig 2022), whilst birds can move more easily across a landscape, and so any benefits of organic management for birds may be hidden within a heterogenous landscape matrix of conventional farms and semi-natural habitats (Batáry *et al.* 2010, Schneider *et al.* 2014, Smith *et al.* 2020, Gong *et al.* 2022). This effect could be further exacerbated in organic vineyards, which have smaller fields (Chapter 3) that could facilitate habitat spill-over and decrease the importance of field-scale variables for bird communities. Additionally, the **smaller fields in organic vineyards increase access of grape-eaters to the crop, which results in higher levels of crop damage and more pronounced yield losses** (Chapter 5), whilst making management more costly and risking soil compaction, particularly in headlands where machinery passes multiple times (Clough *et al.* 2020).

The consideration of finer-scale management practices may be more widely informative for influencing change across farms under various management regimes, which could lead to wider-scale biodiversity benefits. This may be particularly important for the English viticultural industry where management approaches are diverse, and unlike other European viticultural systems (Jeanneret *et al.* 2021), the contrast in management between organic and non-organic vineyards is smaller as, for example, many 'non-organic' vineyards avoid herbicides and limit agrochemical use when possible (Chapter 4, and pers. obs.). Across English vineyards, **we found biodiversity to more strongly respond to an *ecotoxicity score* that we derived from agrochemical use data, and to ground vegetation cover** (Chapter 4), rather than to the overall management regime. Non-organic and SWGB-accredited vineyards are more intensively managed and had significantly higher *ecotoxicity scores*, which may be linked to higher yields due to increased vine vigour achieved through fertilisation (Döring *et al.* 2015, 2019). Future research should aim to disentangle the relative contributions of specific (organic and non-organic) agrochemicals to environmental toxicity, biodiversity conservation and yield to inform which agrochemicals are compatible with sustainable management. Whilst we did not consider the isolated effects of agrochemicals, we did **find a significant negative effect of herbicide use on ground vegetation cover** (Chapter 4), whose impact on biodiversity may be stronger compared to other agrochemicals, such as pesticides, as herbicide action is not targeted to specific plant species (Gong *et al.* 2022). Considering that ground vegetation cover had a consistent, positive effect on vineyard biodiversity (Chapter 4) and without a yield penalty (Chapter 5), strongly points to herbicide use not being compatible with sustainable viticulture.

Biodiversity conservation in viticulture: an outlook

Promoting biodiversity is important across English vineyards and a target within the SWGB-accreditation (pers. comm. and SWGB 2020), and we show that biodiversity can contribute to the creation of multifunctional viticultural landscapes that support production, business prosperity and wider benefits for human wellbeing. We have demonstrated that during the summer months when vineyards are running tours and wine tasking events, **bird species richness enhances soundscape complexity and volume, which has a positive effect of visitors' experience** (Chapter 6), and highlights the importance of vineyards in delivering cultural ecosystem services (Assandri *et al.* 2018). Nonetheless, **at harvest, an influx of grape-eating species inflicts direct crop damage** (Chapter 5), **particularly near woodlands and in fields with more edges**, which are features that earlier research has identified as aesthetically important in vineyards (Assandri *et al.* 2018) and other green spaces (Bratman *et al.* 2019, Zhang *et al.* 2022). This means that evidence-based and targeted management approaches may be necessary to maximise the net benefits of bird communities in vineyards.

Research presented in this thesis has focused on general biodiversity patterns rather than focussing on single species, which has identified key drivers of overall biodiversity that can inform nature-friendly management relevant to the wider industry. Nonetheless, some specific species deserve a mention and to be the subject of more targeted research in the future. **Across English vineyards, we recorded 15 red-listed species**, which included big populations of Eurasian starlings *Sturnus vulgaris,* Common linnets *Carduelis cannabina*, Song thrushes *Turdus philomelos,* House martins *Delichon urbica* and House sparrows *Passer domesticus* (Chapter 4), which suggests that the conservation of some threatened species could be compatible with English viticulture. Nonetheless, we also identified **seven of the red-listed species to be grape-eaters** (Chapter 5), most notably Eurasian starlings. Some of these species' population have steeply declined across European agricultural landscapes due to the loss of shrubland and food resources associated with landscape homogenisation (Sanderson *et al.* 2013, Heldbjerg *et al.* 2019). The relatively heterogeneous nature of English viticultural landscapes could be increasing the suitability of parts of lowland England for some of these species, though, in the case of Starlings, this may also be having negative consequences for crop production. Another example of a species to consider in future research, and broader countryside management in the UK, is the Common pheasant *Phasianus colchicus*, of which 48 million individuals are released each year in the UK for driven game shooting (Aebischer 2019). Pheasants prefer foraging within heterogenous habitats (Schöll *et al.* 2023) and so may be attracted to vineyards, particularly at harvest when we noted Pheasants to account for a relatively high proportion of the grape-eating species (Chapter 5). Hence, whilst English viticulture may be compatible with the conservation of threatened bird species, future research should focus on identifying the drivers of specific species' abundances and activity patterns to inform approaches to minimising disservices to crop production (for examples of management approaches see: Peisley *et al.* 2017, Castañeda *et al.* 2021) without jeopardising the overall suitability of vineyards for biodiversity conservation.

Incorporating biodiversity conservation into agricultural landscapes requires the simultaneous consideration of the effects that management approaches have on biodiversity, ecosystem functioning and on yield, and I propose that the *compatibility index* and *substitution index* proposed by Gong *et al.* (2022) could be used to help decision making. Firstly, the *compatibility index* could be used to evaluate the trade-off between biodiversity gains and yield as might arise from the management of Starlings, where the outcomes of targeted management that result in production gains through reduced crop damage are weighed up against the loss of a threatened species that may be contributing to cultural ecosystem services. Secondly, the *substitution index* considers the consequences of switching between management approaches, and could help determine if adding a wildflower strip between vine field edges and edge habitats (recommended in Chapter 5), would be a worthwhile management approach as whilst it could reduce grape damage and enhance wider biodiversity (our results in Chapter 4 and Griffiths-Lee *et al.* 2023), it may require taking cropland out of production and lead to production losses.

7.2. Broader context: lesson learnt for designing multifunctional landscapes

7.2.1. Informing research

Agroecological studies rarely consider wider societal benefits of biodiversity, and we are not aware of a single other study set within an agricultural landscape that considered multiple ecosystem benefits, including those not directly linked to agriculture. The theoretical framework for assessing multiple nature contributions to people is in place (Pascual *et al.* 2017), and could be supported by emerging technologies and tools, such as passive acoustic monitoring and the use of acoustic indices to monitor species richness (Chapter 6), which could replace, or supplement, in-depth ecological surveys. Moreover, scientific studies often make generic and generalised recommendations that farmers do not associate with, and all too frequently focus on the ecological benefits without translating them to yield impacts and resulting financial gains or losses (Garibaldi *et al.* 2017), both of which limit practice uptake (Kleijn *et al.* 2019). This is partly due to logistical, time and financial constraints associated with typical research grants, which have also applied to this thesis. Learning from my research, I make the following research recommendations for better informing biodiversity management across multifunctional landscapes*:*

(i) to increase generalisability of results and optimise data collection, stratified sampling and evidence-informed approach to study design is necessary (Chapter 2);

(ii) the relevance of research to industry and the uptake of results can be increased by engaging with stakeholders and farm managers to identify key issues and to develop research programmes (see SUFICA approach, Appendix 1);

(iii) to maximise the benefits of biodiversity within agricultural landscapes, robust sampling of communities and quantification of ecosystem service and disservice are required and should take place across multiple scales and years (Chapters 4-6, though increasing the number of sampling years, taxa, and ecosystem services and disservices that were measured would be an improvement);

(iv) to improve generalisability of results and to identify the direct drivers of biodiversity, there should be a shift away from studying general and not clearly defined management regimes (e.g. organic management), and instead a combination of specific management practices should be directly measured (Chapters 4-5 partially achieve this, though management practices could be measured more robustly, for example through direct soil ecotoxicity measurements);

(v) direct quantification of production outputs (yields) is required, as is the consideration of the costs of inputs across the whole production chain (e.g. for any management approach, the costs of management of a hectare of land, including the cost of agrochemical inputs and manpower to deliver necessary management, should be offset against the financial gains from crop and product sales and the tourism industry).

7.2.2. Informing policy and management

The success of implementing biodiversity-conservation measures across multifunctional landscapes and to increasing the benefits of biodiversity to agriculture, relies on the uptake of evidence-based, specific and unambiguous actions that schemes often lack (Sigwalt *et al.* 2012, SWGB 2020). For example, the Sustainable Wines of Great Britain accreditation scheme guidelines do not specify any minimum requirements, whilst our results, strongly suggest that herbicides should not be used across vineyards aiming to become biodiversity friendly (see section 7.2.2.). Secondly, scheme guidelines often include broad recommendations, such as '*create new habitats in order to increase biodiversity, such as hedges',* and 'i*nstall at least one nesting box and bat box per parcel'*, which without further scientific evidence could have detrimental consequences, as planting hedges in the wrong place may jeopardise habitat suitability for open-habitat specialists (Assandri *et al.* 2016, Pithon *et al.* 2016), whilst placing nest boxes of the wrong design or in the wrong location could attract non-target species that disadvantage production (e.g. European starlings). Such poor management choices can lead to a loss of resources and time and decrease the likelihood that a farmer engages in future conservation initiatives. The difficulty lies in the fact that whilst management recommendations need to be specific, they also need to be flexible enough to enable context-specific practice uptake, and I suggest that research-focused industry schemes that work alongside wider governmental payment-schemes could make this possible. To achieve this, impact and compliance with guidelines should be monitored and rewarded through premium prices or higher-tier payments, and secondly, by engaging with researchers, industry associations could promote context-specific research to address knowledge gaps and support the uptake of evidence-based and targeted practices (Batáry *et al.* 2015, Stout & Dicks 2022). This may also help address the current issue of farmers having a lot of flexibility in deciding which areas of sustainability they would like to engage in, which usually results in a focus on low-yielding areas and on practices that do not interfere with management (Sigwalt *et al.* 2012, Kleijn *et al.* 2019), which can lead to low biodiversity gains.

Land-sharing approaches are commonly supported through payment schemes, which have underpinned most conservation efforts across agricultural landscapes, and voluntary standards and certifications focussing on sustainable agriculture have received a lot of societal and governmental support (Pullin & Knight 2009, Casalegno *et al.* 2022, Gomes *et al.* 2023). For example, the European Commission has set out an ambitious plan for 25% of European agricultural landscapes to be organically managed by 2030, whilst the sales of organic products across Europe are increasing (European Commission 2023). As our research has shown, these one-size-fits-all general management approaches are not guaranteed to be nature-friendly and on their own, they are not the solution to the biodiversity crises. For example, even if organic management had an unambiguous positive effect on biodiversity, most landscapes and biodiversity would still be shaped by the 75% of land under conventional agriculture. Additionally, as we have demonstrated in Brazilian fruit farms and English vineyards, not all species are compatible with agriculture, either because they require undisturbed native habitats, or because they are associated with disservices. Moving forward, a set of approaches needs to be integrated to deliver *multifunctional landscapes,* which could be supported through a tiered payment system, such as the new Environmental Land Management Scheme (ELMS; DEFRA 2023) in England, complimented by industry-specific schemes. I suggest, this could be structured as follows:

(i) The first tier (as in the Sustainable Farming Incentive of ELMS) could focus on supporting adoption of sustainable approaches across agricultural land that maintain or enhance productivity (e.g. promoting ground vegetation cover in vineyards), which would mirror much of the current strategies for biodiversity conservation in agricultural landscapes. These strategies could focus on supporting specific ecosystem service providers if these have been identified, though the conservation of 'common' species, many of which have been rapidly declining across agricultural landscapes (Donald *et al.* 2001, Inger *et al.* 2015), should not be overlooked, as these species contribute most to ecosystem service provision (Gaston 2011), and when knowledge on the contributions of specific species is lacking, their conservation is most important for ecological intensification.

(ii) The second tier (as in the Countryside Stewardship tier of ELMS) could focus on wider-scale approaches that support coordinated actions across an industry, such as viticulture in Southern England. For example, some species do less well within a fragmented matrix of agricultural and semi-natural habitats, and may benefit more from wider areas of lower-yielding and non-farmland habitat being left (Assandri *et al.* 2018, Finch *et al.* 2019, Casas *et al.* 2020). Such approaches could be coordinated by industry-specific schemes and networks to enable clustering of intensively managed farmland, whilst compensation schemes could support the maintenance of lower yielding farmland.

(iii) The third tier (Landscape Recovery projects in ELMS) could focus on the retention of non-agricultural habitats that are necessary for the conservation of species not compatible with agriculture, and to protect the cultural, aesthetic value of pristine habitats. This could be further supported by a wider introduction of concessions for the purchase and sale of agricultural land, as has been required by the European Commission since 2016 (EU 1308/2013), which could see the inclusion of ecological requirements that prevent the creation of new, or intensification of traditional, farmland within areas that are suitable habitat for priority conservation species.

7.3. Beyond multifunctional landscapes

Biodiversity conservation within agricultural landscapes needs to break boundaries and be seen as more than an agroecological issue. Counting biodiversity within one country does not make sense when halting expansion or intensification in one region can be achieved through displacement of agriculture to another country (Pfaff & Walker 2010, Marselis *et al.* 2017).

Moreover, the pressure that agricultural landscapes are under stems from the ever-growing demand for goods (Godfray *et al.* 2010), which is not only fuelled by the growing human population but also by shifting dietary habitats, namely overconsumption of calories (Bodirsky *et al.* 2020) and increased intake of 'luxury' products, which have been the focus of this thesis. All of this is taking place whilst almost 10% of the global human population are facing food shortages (United Nations 2022), and whilst increasing yields through intensification and lowering food prices is crucial to reaching global food equality, caution should be taken in how this may be fuelling the 'cheaper food' paradigm, where lower food prices increase consumption and result in increased demand (Byerlee *et al.* 2014). Whilst it may be essential to retain high yields of staple foods that provide most of the global nutrition and calories, widespread adoption of nature-friendly farming practices may only be possible alongside dietary changes and decreases in food waste (Bodirsky *et al.* 2020, Dasgupta 2021). Such societal change could be incentivised through higher product prices of luxury goods, which could reward the uptake and investment in more biodiversity-friendly and sustainable farming approaches that could lead to an income gap for farmers if the diversification of farming reduced yields (at least in the short term; Rosa-Schleich *et al.* 2019). This may require increased education of the benefits of diversified farming approaches, as the majority of consumers in some of the world's most developed countries, such as the United States, have indicated unwillingness to pay more for sustainably-produced luxury products, including alcohols (Sánchez-Bravo *et al.* 2021), which could be caused by the strong disconnect between people, food production and nature in these countries (Kesebir & Kesebir 2017, Ives *et al.* 2018, Kirchweger 2021). A shift towards *multifunctional landscapes* that integrate agricultural land with space for recreation, which our research has demonstrated may be feasible within the viticultural industry, could address this disconnect, whilst supporting production, biodiversity and wider wellbeing benefits.

Reference list

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