An assessment of relative habitat use as a metric for species' habitat association and degree of specialization

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ABSTRACT

In order to understand species' sensitivity to habitat change, we must correctly determine if a species is associated with a habitat or not, and if it is associated, its degree of specialization for that habitat. However, definitions of species' habitat association and specialization are often static, categorical classifications that coarsely define species as either habitat specialists or generalists and can fail to account for potential temporal or spatial differences in association or specialization. In contrast, quantitative metrics can provide a more nuanced assessment, defining species' habitat associations and specialization along a continuous scale and accommodate for temporal or spatial variation, but these approaches are less widely used. Here we explore relative habitat use (RHU) as a metric for quantifying species' association with and degree of specialization for different habitat

types. RHU determines the extent of a species' association with a given habitat by comparing its abundance in that habitat relative to its mean abundance across all other habitats. Using monitoring data for breeding birds across Europe from 1998 to 2017; we calculate RHU scores for 246 species for five habitat types and compared them to the literature-based classifications of their association with and specialization for each of these habitats. We also explored the temporal variation in species' RHU scores for each habitat and assessed how this varied according to association and degree of specialization. In general, species' RHU and literature-derived classifications were well aligned, as RHU scores for a given habitat increased in line with reported association and specialization. In addition, temporal variation in RHU scores were influenced by association and degree of specialization, with lower scores for those associated with, and those more specialized to, a given habitat. As a continuous metric, RHU allows a detailed assessment of species' association with and degree of specialization for different habitats that can be tailored to specific temporal and/or spatial requirements. It has the potential to be a valuable tool for identifying indicator species and in supporting the design, implementation and monitoring of conservation management actions.

1. Introduction

There is growing recognition that continued biodiversity declines and loss of species through land-use change and habitat degradation are occurring in a non-random manner, with specialist species' populations declining at faster rates compared to generalist species (Devictor et al., 2010). Accurately assessing species' specialization is therefore vital to better understand their potential sensitivity to changes in the quantity or quality of available habitat and their vulnerability to population declines. However, assessments of specialization are often categorical, with species grouped into those that are associated with or are not associated with a given habitat, and whether those that are associated are habitat specialists or generalists (Fridley et al., 2007; Devictor et al., 2008, 2010; Chazdon et al., 2011; Herrando et al., 2016; Morelli et al., 2019). Specialism itself is also characterised in two dimensions - specialist species are defined as those whose populations are restricted to a smaller range of habitats and/or use a small portion of the resources that are available in a habitat (Reid et al., 2005; Smart et al., 2006; Devictor et al., 2008). By comparison, generalist species are defined as those that are capable of exploiting a range of habitats, and/or use a larger number of the available resources in a habitat (Morelli et al., 2019); here we focus on definitions of specialization that are based on the range of habitats a species uses rather than resource use within habitats. Assessments of habitat association and specialization are often derived from expert opinions, observations or small-scale field studies (Thogmartin and Knutson, 2007; Redhead et al., 2016), and are generally applied at the species level. As a result, phenotypic plasticity in response to temporal and spatial changes in environmental conditions, which may cause variation in a species' realized niche and therefore in its association with and specialization for a given habitat, can be overlooked (Devictor et al., 2010). In addition, categorical classifications that simply define a list of species as specialized to a given habitat fail to acknowledge that there is variation between species in their degree of specialization for that habitat, and that this may have an important effect on their population trends over time (Reif et al., 2008).

A number of quantitative metrics that can account for temporal and spatial variation in association and specialization and allow between-species comparisons have been proposed (Julliard et al., 2006; Devictor et al., 2008; Reif et al., 2008; Larsen et al., 2011; Renwick et al., 2012; Rivas-Salvador et al., 2019). Simple metrics such as Simpson's and Shannon's Diversity Indices (Levins, 1968), which follow Levins' measure of niche breadth, quantify specialization as the number of habitats used by a species, relative to the total number of habitats available (Levins, 1968). These metrics are both easy to explain and calculate and can accommodate presence/absence or abundance data (Devictor et al., 2010). However, they can be subject to sampling biases and limitations, particularly as both indices calculate specialization on the assumption that all habitats are equally available (Petraitis, 1979). Julliard et al. (2006) presented an alternative approach, the Species Specialization Index (SSI), which quantifies species' degree of specialization for a given habitat as the coefficient of variation (standard deviation/mean) in

species' abundance across habitats. Low SSI scores infer that there is little variation in a species' abundance between habitats, and that the species is more general in its habitat use, while high SSI scores imply that a species has a high abundance in a limited number of habitats and is therefore more specialized (Julliard et al., 2006; Devictor et al., 2008). This approach minimises the limitations of Simpson's and Shannon's Indices by avoiding the assumption that habitats are equally available (Hayward et al., 2006; Julliard et al., 2006). However, SSI only gives a single score per species, defining its overall degree of specialization rather than its specialization for individual habitats (Julliard et al., 2006; Reif et al., 2010). Furthermore, while SSI calculates specialization based on variation in species' abundance across habitats, this can present limitations if based on only a small number of sites for that habitat or if there are differences in sample size of sites between habitats (Morelli et al., 2019). Renwick et al. (2012) provide an alternative to SSI that accounts for the sample size of sites by adapting Jacobs' Preference Index (Jacobs, 1974), which determines species' specialization for a habitat by comparing the proportion of habitat used to the proportion of habitat available. Jacobs' Index does not account for species' abundances across habitats, but Renwick et al. (2012) adapted the index by comparing species' counts on sampled transects in sites of a target habitat to species' counts that would otherwise be found from random surveying of sites. Species with a significantly higher proportion of counts in sites of the target habitat were classified as being specialized to that habitat. Whilst accounting for the number of sites sampled improves on SSI, Renwick et al.'s (2012) approach still only allows us to determine if a species' is specialized or not to a habitat of particular interest. It is not calculated in such a way that allows us to explore the extent of species' specialization for each individual habitat.

The relative habitat use (RHU) metric was introduced by Larsen et al. (2011) as an alternative approach to quantifying species' habitat association and degree of specialization. RHU is derived from the SSI measure but is computed for each habitat in turn, allowing for cross-habitat comparisons. Specifically, it measures a species' association with a given habitat as its abundance in that habitat relative to its mean abundance in all other habitats, accounting for both the total number of sites and the number of sites of that specific habitat surveyed. An RHU score of less than one infers a weak association with a habitat, one to two as a moderate association, and greater than two as a strong association with the habitat (Eskildsen et al., 2013). The number of habitats a species is identified as having an association with (RHU $\geq$ 1) indicates its degree of habitat specialization. This metric can be calculated at any temporal and/or spatial scale, allowing comparisons in RHU scores to be made across time and space. Larsen et al. (2011) applied this approach to the Danish avifauna, identifying sets of specialist forest birds and farmland birds that differed to those derived from categorical-based assessments that relied on expert opinions. The index for forest habitat based on the RHU approach saw an overall negative trend, while the index for the categorical-based approach remained stable over time.

In this paper, we explore the performance of RHU as a metric for quantifying species' habitat association and degree of specialization

more generally and explore variation in species' RHU scores over time. First, we assess the relationship between RHU and existing categorical classifications of species' habitat associations that are derived from the literature. We predict that species' RHUs should be higher for those habitats that they have been reported in the literature as being associated with than those habitats with no reported association. Second, we assess the performance of RHU in quantifying degree of habitat specialization by comparing RHU scores for more specialist species *i.e.*, those reported in the literature as only being associated with one habitat to more generalist species *i.e.*, those reported in the literature as being associated with that habitat plus one or two others, hypothesising that species more specialized to a given habitat will have a higher RHU for that habitat than more generalist species. We then assess the influence of habitat association and degree of specialization on temporal variation in RHU scores to examine its stability and consistency.

We use long-term monitoring data for breeding birds across Europe, collected and collated under the Pan-European Common Bird Monitoring Scheme (PECBMS: https://pecbms.info/about-us/; Brlík et al., 2021), to calculate RHU scores for each species. Birds are commonly used as indicator species due to their sensitivity to environmental changes and well-studied ecology, physiology and behaviours (Gregory et al., 2005; BirdLife International, 2020). PECBMS data are used to produce i) individual species population trends at Pan-European levels, and ii) multi-species composite indices for all common bird species, and for subsets of species categorized as being associated with forest and farmland habitats (Gregory et al., 2005; Gregory et al., 2019). These indices in turn support EU biodiversity targets across national, regional, and European spatial scales (EEA, 2012; Fraixedas et al., 2020), and can be used to monitor the effects of management practices on bird species (Wade et al., 2013, 2014; Gamero et al., 2017). Objectively quantifying the extent of species' association with and degree of specialization for different habitats could advance our understanding of individual species' vulnerability to environmental changes and management practices. Furthermore, these metrics could be used to underpin the selection of species for inclusion in multi-species indicators, for monitoring biodiversity health and measuring progress towards biodiversity conservation targets (Pereira and Davidcooper, 2006; Niemeijer and de Groot, 2008; Walpole et al., 2009; Larsen et al., 2011).

2. Methods

2.1. Count data

We use annual, site-level count data for breeding birds from 19 monitoring schemes in 17 countries across Europe collated by PECBMS. In each scheme, species are surveyed using one of three possible techniques; point count, line transect or territory mapping (Brlík et al., 2021). The geographical coordinates of the centroids of each survey site (22,710 sites in total) are known, with count data from 1998 to 2017 used here to ensure coverage from a representative suite of countries. Of the 426 species recorded by the national monitoring schemes during this period, we removed introduced species *i.e.*, those introduced outside of its historical distribution range through direct or indirect human activity (23), and locally specific species *i.e.*, those only found in a small area of one country (7). Subspecies were grouped at species level (Handbook of the Birds of the World and BirdLife International, 2020).

2.2. RHU calculation

We extracted Level three habitat data from Corine Land Cover (CLC) 2012 (Copernicus Land Monitoring Service, 2012) for circular 1 km^2 areas centred on each PECBMS survey site; the habitat encompassed was taken as representative of that covered during bird surveys at that site. Open marine habitat was not the focus of this study, therefore any sites containing lagoons, estuaries, and/or sea/ocean habitats (822 in total) were removed from further analysis. In the remaining sites, habitats

were aggregated into five broad types; forest, farmland, urban, wetland (including inland freshwater and coastal and inland wetlands) and semi-natural (including natural grasslands, moors, heathland, sclerophyllous vegetation and sparsely vegetated areas) (Further details in Table A1.). The total areas of each of these five habitat types present at each site were calculated and sites were classified according to the dominant habitat type, *i.e.*, that which covered the largest area within each site. For each species in turn, RHU in each year t was calculated as:

$$RHU_{i,t} = \frac{n_{i,t}/p_{i,t}}{(N_t - n_{i,t})/(P_t - p_i, t)}$$

where i is the ith habitat, n_i = number of individuals in the ith habitat, p_i = number of sites of the ith habitat, N_t = total number of individuals and P_t = total number of sites surveyed in year t (Larsen et al., 2011). To ensure only data from potentially available sites were included in each species' RHU calculations, P_t was calculated as the sum of all sites surveyed in year t that fell within a 50 km radius buffer of sites occupied by a given species in year t.

For each species, RHU for each of the five habitat types were calculated at the European level. RHU scores can be sensitive to changes in $p_{i,t}$ especially when P_t is small, so we imposed minimum site thresholds, both across and within habitats, for a species' inclusion in subsequent analyses. RHU scores were only calculated for a given species in a given year if that species was recorded in at least 35 sites in that year, with RHU for an individual habitat only calculated if the species was recorded in at least seven sites of that habitat type in that year ($p_{i,t}$). We also specified that these site thresholds had to be met in at least three years across the 20-year period for a species to be included in our analyses. This excluded 150 species from further analyses. For the remaining 246 species, if a species was recorded in a given habitat in a given year, but at fewer than seven sites, it was assigned an "n/a" RHU score for that habitat in that year. If a species was recorded in at least 35 sites in a given year but was not recorded at all in a given habitat, the species received an RHU score of zero for that habitat in that year. Very high RHU scores can potentially arise if the relative number of individuals recorded in ith habitat is particularly high, especially if the proportion of ith habitat sites is low. We therefore imposed a maximum RHU of five, with any scores above this assigned this value. Setting this maximum identified species with a very strong association with a given habitat without extremely high RHU scores skewing results. RHU scores cannot be calculated if a species is only recorded in one habitat type in a given year. In such instances, if the species was recorded in at least 35 sites of that habitat type in a given year, an RHU score of five was assigned to that species for that habitat in that year, with an RHU score of zero for all other habitats.

We recognise that classifying sites by the dominant habitat type does not necessarily capture the association of individual birds with specific patches of habitat, which may or may not be the dominant habitat type. It is therefore important to emphasise that the habitat associations reported here represent associations with landscapes dominated by a given land cover type. Habitat is a complex multidimensional concept (Kirk et al., 2018), but CLC classes, based on remote sensing to determine land cover types is commonly used as a proxy for habitat (Lumbierres et al., 2021). Given the spatial and temporal scale of the data used and that the average area covered by the dominant habitat type was, for forest sites: 78.4% ± 0.251%, farmland sites: 86.2% ± 0.158%, urban sites: 82.7% ± 0.384%, wetland sites: 77.9% ± 0.545% and semi-natural sites: 80.0% ± 0.419% (Fig. A1), any associations with a particular land cover type identified here infer that a substantial proportion of a species population is likely to be influenced by processes and management associated with that dominant habitat. For example, forest specialists are unlikely to be recorded in large numbers in sites dominated by habitats other than forest, relative to their counts in forest sites, so high RHU scores will only be derived for forest habitats. If, however, a species is found both in large tracts of forest and smaller forest plots or hedgerows within farmland dominated landscapes, associations with both forest and farmland habitat may be identified.
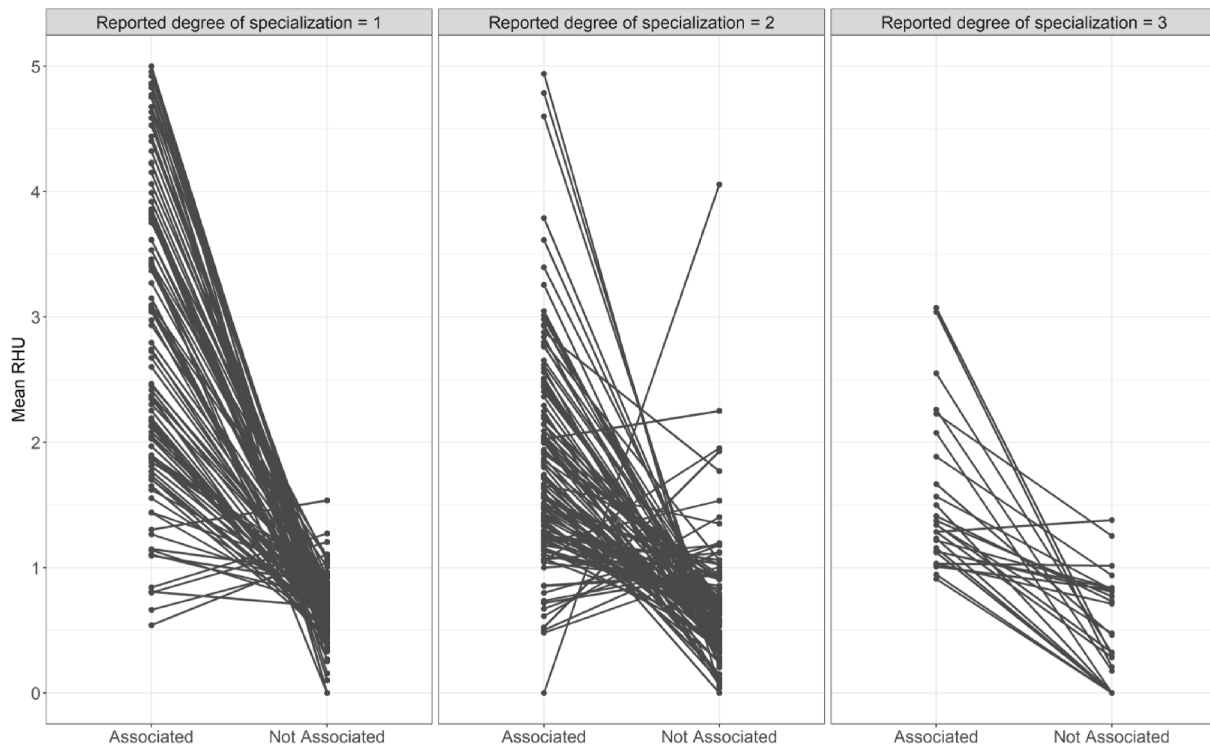
Fig. 1. Species' mean relative habitat use (RHU) scores for habitat(s) they were reported in the species-habitat database (Roscher et al., 2015) as being associated with, versus their mean RHUs for habitats they were not reported as being associated with. Lines connect scores for individual species. Panels show results for species grouped according to their reported degree of habitat specialization *i.e.* reported as being associated with a single habitat (Reported degree of specialization = 1), associated with two habitats (Reported degree of specialization = 2) or associated with three habitats (Reported degree of specialization = 3).

Nonetheless, the farmland RHU score for such a species would still only exceed one (inferring at least a moderate association) if the proportion of total individuals found on farmland sites was greater than the proportion of total sites surveyed that were defined as farmland. Thus, a farmland RHU ≥ 1 would only be generated i) if the species is widespread across farmland sites and ii) occurs in sufficient numbers in farmland sites containing patches of suitable habitat to offset its absence from farmland sites that do not contain any suitable habitat. The species is therefore likely to also be vulnerable to management or environmental changes occurring in farmed landscapes (Boutin and Jobin, 1998; Gove et al., 2007).

2.3. Existing categorical classifications of habitat association

Categorical habitat associations for each species were extracted from a database built to support the European Environment Agency's goal to report on the state and trends of biodiversity from an ecosystem perspective, with ecosystems defined at the scale of habitat/biotope or landscape and classified by Level three CLC habitats (Maes et al., 2020; Roscher et al., 2015). This database reports species' associations with urban, cropland, grassland, woodland & forest, heathland & shrub, sparsely vegetated land, wetlands and rivers & lakes, with associations reported at the European scale and derived from multiple published sources; Hagemeijer and Blair (1997); Tucker and Evans (1997); Mullarney, Svensson and Zetterström (2009). From this, each species was reported as associated with a maximum of three of these habitat types. To allow direct comparison with RHU scores, we aggregated reported associations into the five over-arching habitat types outlined in section 2.2 and for which species' RHUs were calculated. Specifically, we combined grassland and cropland as farmland habitat, heathland & shrub and sparsely vegetated land as semi-natural and wetlands and rivers & lakes as wetland. Urban and woodland & forest (hereafter forest) remained as they were. The number of habitats each species was

recorded as being associated with was used to define its degree of habitat specialization. Hereafter, we refer to these associations as 'reported'. For example, middle-spotted woodpecker (*Leiopicus medius*) is reported as only being associated with forest, great tit (*Parus major*) is reported as being associated with both forest and urban habitats, and serin (*Serinus serinus*) is reported as being associated with forest, urban, and farmland. Whilst all three are reported as associated with forest, middle-spotted woodpecker is taken as the most specialized and serin as the most generalist of the three due to their additional habitat associations.

2.4. Data analysis

All calculations of RHU and statistical analyses were conducted using R version 4.0.1 (R Core Team, 2020).

2.4.1. RHU versus literature-based measures for habitat association

Species' RHU scores for each habitat were calculated annually using European-level data and averaged across all years to produce mean RHU scores for each habitat. We first identified all species reported in the species-habitat database (Roscher et al., 2015) as being associated with only one habitat *i.e.,* most specialist species and compared their mean RHU for that habitat with their mean RHU across the other habitats for which scores were available. We then identified all species reported in the database (Roscher et al., 2015) as being associated with i) two habitats and ii) three habitats and compared their mean RHU scores across those associated habitats with their mean RHU across the other habitats. Data were not normally distributed, so paired sample Wilcoxon tests were used to compare species' mean RHUs for "associated" and "not-associated" habitat(s).

Second, for species reported as associated with only one habitat we also quantified how often this habitat also had the highest mean RHU score. For species reported as being associated with two habitats, we quantified how often their mean RHUs for those habitats filled the first and second positions
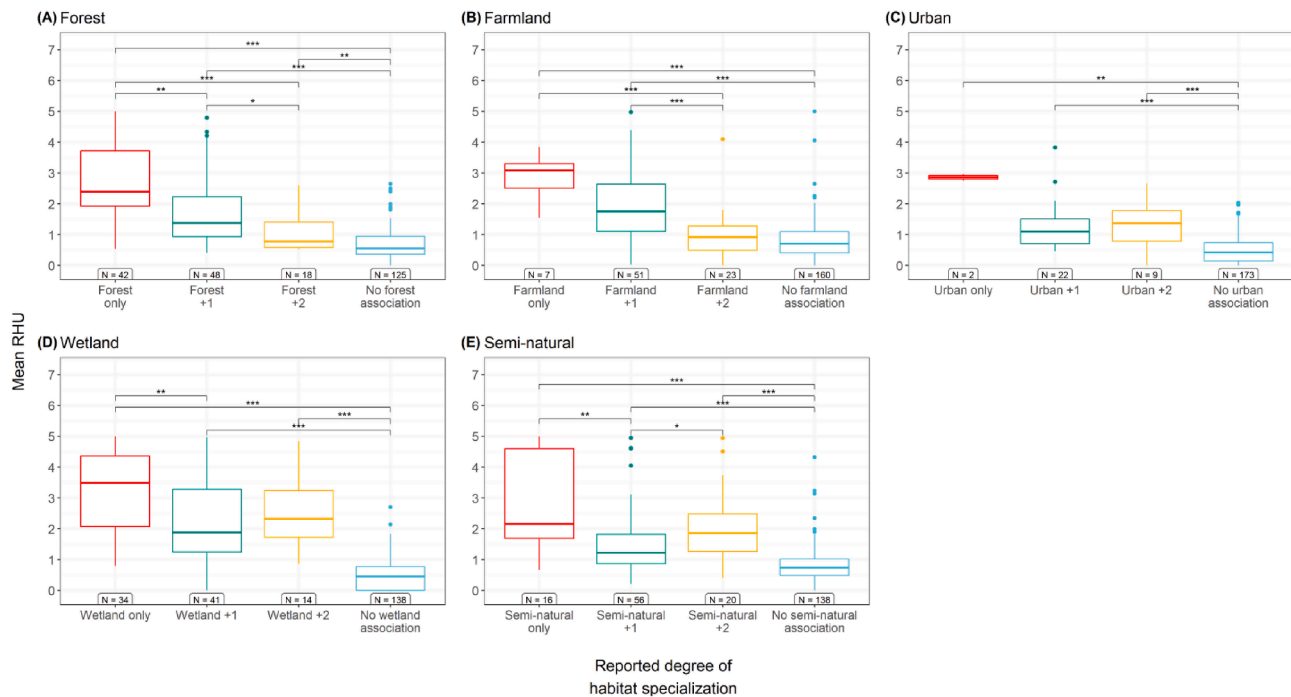
Fig. 2. Species mean relative habitat use (RHU) scores for A) forest; B) farmland; C) urban; D) wetland and E) semi-natural habitats. Within the panel for each habitat, species are grouped according to their reported degree of habitat specialization, determined by the number of habitats they have been reported as being associated with or if not reported as being associated with the panel habitat (Roscher et al., 2015). Sample size for each group is given under each boxplot. Pairwise comparisons showing significant differences are also identified (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Table 1

Estimated model parameters, standard errors, t-values and p-values from GLMs examining the influence of habitat association and degree of habitat specialization on RHU-CV_t. Separate models were run with i) species' association with that specific habitat, defined by mean RHU score for that habitat (Not associated = mean RHU < 1, Associated = mean RHU ≥ 1) and ii) for those species associated with a given habitat, their degree of specialization, defined as the total number of habitats for which they had a mean RHU ≥ 1, as fixed effects. Significant terms are highlighted in bold.

Habitat	Predictor	Term	Estimate	std. error	t -statistic	p-value
Forest		Intercept	0.310	0.015	21.223	**<0.001**
	Association	Associated	−0.050	0.021	−2.356	**0.019**
		Intercept	0.184	0.029	6.305	**<0.001**
	Degree of habitat specialization	Two habitats	0.092	0.036	2.561	**0.012**
		Three – Four habitats	0.108	0.038	2.807	**0.006**
Farmland		Intercept	0.352	0.019	18.389	**<0.001**
	Association	Associated	−0.104	0.029	−3.607	**<0.001**
		Intercept	0.233	0.026	8.900	**<0.001**
	Degree of habitat specialization	Two habitats	0.012	0.034	0.350	0.727
		Three – Four habitats	0.046	0.041	1.124	0.264
Urban		Intercept	0.363	0.025	14.629	**<0.001**
	Association	Associated	−0.119	0.048	−2.460	**0.015**
		Intercept	0.158	0.197	0.800	0.428
	Degree of habitat specialization	Two habitats	0.065	0.201	0.324	0.748
		Three – Four habitats	0.139	0.205	0.677	0.502
Wetland		Intercept	0.369	0.028	13.012	**<0.001**
	Association	Associated	−0.027	0.039	−0.690	0.491
		Intercept	0.198	0.072	2.748	**0.007**
	Degree of habitat specialization	Two habitats	0.158	0.078	2.033	**0.045**
		Three – Four habitats	0.156	0.079	1.966	0.052
Semi-natural		Intercept	0.317	0.017	19.110	**<0.001**
	Association	Associated	0.011	0.024	0.458	0.647
		Intercept	0.194	0.060	3.255	**0.002**
	Degree of habitat specialization	Two habitats	0.120	0.064	1.872	0.064
		Three – Four habitats	0.193	0.067	2.901	**0.005**

when ranking RHUs for all habitats, and for species reported as having three habitat associations, we quantified how often those three habitats were ranked as the top three when ranking mean RHUs for all habitats.

2.4.2. RHU for species' literature-based degree of habitat specialization

For each habitat in turn, we compared the mean European-level RHUs of species reported as being i) only associated with that habitat, ii) associated with that habitat plus one other, iii) associated with that habitat plus two others, and iv) not reported as associated with that habitat. Mean RHU scores were not normally distributed so non-parametric Kruskal Wallis tests were used, with post-hoc Dunn's tests for pairwise comparisons (R package dunn.test version 1.3.5, Dinno, 2017).
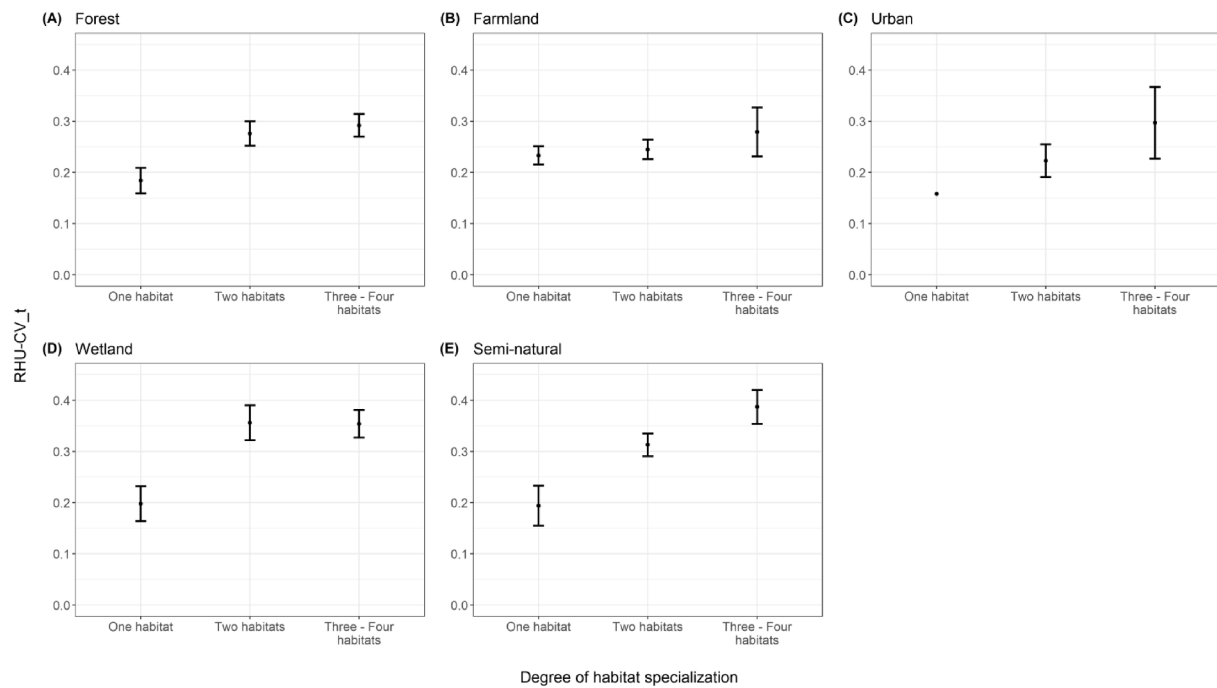
Fig. 3. Mean coefficient of variation in relative habitat use over time (RHU-CV_t ($\pm$SE)) for species associated with A) forest; B) farmland; C) urban; D) wetland and E) semi-natural habitats, according to their degree of habitat specialization, defined as the total number of habitats for which they had a mean RHU $\geq$ 1.

2.4.3. Temporal variation in RHU

Using species' mean, European-level RHU across all years, we reclassified species' habitat associations according to RHU scores alone. In line with Eskildsen et al. (2013), species were categorized as associated with a given habitat if their mean RHU score for that habitat was $\geq$ 1 and not associated with the habitat if mean RHU was $<$ 1. For those associated with a given habitat, we classified their degree of habitat specialization according to the number of habitats for which they demonstrated a mean RHU $\geq$ 1. For each habitat in turn, we then explored the temporal stability of species' RHU scores according to their association with and degree of specialization for that habitat. For each habitat, we calculated the coefficient of variation (hereafter CV) in each species' RHU over time (RHU-CV_t) as the standard deviation in its annual European-level RHU scores for that habitat, divided by its mean RHU for that habitat across years. For each habitat in turn, a GLM was then built with species' RHU-CV_t for that habitat as the dependent variable and *habitat association* (categorical term, with 'Not associated' if mean RHU $<$ 1 and 'Associated' if mean RHU $\geq$ 1) as the fixed effect. For those species associated with a given habitat, a second GLM was built with species' RHU-CV_t for that habitat as the dependent variable and *degree of habitat specialization* (categorical term, with three levels, reporting the total number of habitats with mean RHU $\geq$ 1 *i.e.* one, two or three-four) as the fixed effect. Only one species, *Mergus merganser* (Goosander) demonstrated mean RHU scores $\geq$ 1 for four habitats, so this was grouped with species with mean RHU $\geq$ 1 for three habitats.

3. Results

3.1. RHU-based versus literature-based measures of habitat association

Species had significantly higher RHUs for habitats they were reported as being associated with compared to RHUs for habitats they were not reported as being associated with (*One habitat: Mean RHU Associated $\pm$ SE = 2.921 $\pm$ 0.12, Not associated = 0.669 $\pm$ 0.03, Paired Wilcoxon test: V = 5114, p < 0.001; Two habitats: Mean RHU Associated = 1.836 $\pm$ 0.08, Not associated = 0.688 $\pm$ 0.05, Paired Wilcoxon test: V = 6148, p < 0.001; Three habitats: Mean RHU Associated = 1.548 $\pm$ 0.12, Not associated = 0.498 $\pm$ 0.08, Paired Wilcoxon test: V = 376, p < 0.001*).

The difference between mean RHUs for associated and not associated habitats decreased as the number of habitats a species was reported as being associated with increased (Fig. 1). Four species were excluded from this comparison because they either only had "n/a" RHU scores for associated habitat(s) (three species) or for not associated habitats (one species) due to them not meeting the site thresholds (see Methods).

Of the 101 species reported as being specialized to a given habitat, the RHU for this habitat was the highest of their RHUs for any of the five habitats in 89.1% of cases. For the 113 species reported as being associated with two habitats, these habitats had the highest and second highest RHU scores in 50.4% of cases. For the 28 species reported as being associated with three habitats, these habitats had the three highest RHU scores in 39.3% of cases. The full list of Pan-European RHU scores for each species, in each of the five over-arching habitat types are given in supplementary material, along with the literature-based association classification for each habitat type (Table A2).

3.2. RHU for species' literature-based degree of habitat specialization

Species' RHUs for a given habitat were higher if they were reported as more specialized to that habitat and were always significantly higher than those for species not reported as being associated with that habitat (Fig. 2, Table A3). Species reported as more specialized to forest habitat had significantly higher RHUs than more generalist species reported as being associated with forest (Fig. 2A). Similarly, species specialized to wetland or semi-natural had significantly higher RHUs than more generalist species associated with wetland or semi-natural and one other habitat (Fig. 2D, 2E). Species specialized to farmland had significantly higher RHUs than generalist species associated with farmland and two other habitats (Fig. 2B). Furthermore, species reported as being associated with farmland or forest and one other habitat had significantly higher RHUs than more generalist species associated with either farmland or forest and two other habitats. In contrast, species associated with semi-natural habitat and one other, had significantly lower mean RHU scores than more generalist species associated with semi-natural habitat and two others (Table A3).

3.3. Temporal variation in RHU

RHU-CV_t for species associated with farmland or urban habitats were significantly lower than species not associated with these habitats, but it did not vary significantly according to degree of specialization (Table 1). RHU-CV_t for species associated with forest habitats was significantly lower than for species not associated with forests and also declined as degree of specialization for forest increased (Table 1; Fig. 3A). For wetland and semi-natural habitats, there was no significant difference in RHU-CV_t between associated and not associated species, but more generalist species with a degree of specialization of two and three – four habitats respectively had significantly higher RHU-CV_t scores than those more specialized to wetland or semi-natural (Table 1; Fig. 3D, E).

4. Discussion

We show that RHU and literature-derived classifications for habitat association and degree of specialization are generally well aligned, although there are some disparities. Overall, species demonstrate higher RHU scores for habitat(s) they are reported as being associated with in the literature. Similarly, species reported as being associated with a given habitat have higher RHUs for that habitat compared to species not reported as being associated with it. RHU also differentiates species according to their degree of habitat specialization, with species more specialized to a given habitat having higher mean RHU scores for that habitat than more generalist species that are associated with it. Finally, we show that within the temporal scale of this study, species associated with a given habitat show lower variation in RHU scores for that habitat over time compared to species not associated with it. Furthermore, species more specialized to a given habitat show less variation in their RHUs for that habitat over time compared to more generalist species.

We expect literature-based classifications and RHU to align with one another as both methods rely on observations of species' abundances across habitats to characterise their habitat associations. However, we do identify some instances where RHU and literature-based classifications differ, which are likely to be driven by data collection methods and habitat classification, as well as the specific ecology of individual species. For example, we find that 29 out of 34 species reported as being specialized to wetland habitats also have mean RHUs ≥ 1 for at least one terrestrial habitat (*i.e.* forest, farmland, semi-natural and urban). Furthermore, for five of these 29 species, their RHUs for at least one terrestrial habitat is greater than their RHUs for wetland habitat. This suggests that these "wetland" species are counted in higher numbers in terrestrial habitats than is expected given relative habitat availability. It is important to note that the number of wetland dominated sites surveyed is considerably lower than the number of terrestrial dominated sites surveyed (Table A4). This is due to the fact that the national monitoring schemes are targeted towards terrestrial habitats and therefore more terrestrial species. In addition to this, these "wetland" species may also be counted on patches of wetland habitat within sites dominated by a terrestrial habitat. In this study, RHU calculates species' association with landscapes dominated by a given habitat. In contrast, literature-based classifications for species' habitat associations are derived from observations of species' use of particular habitat types. It is therefore likely that these wetland species are counted in higher numbers on wetland patches within terrestrial dominated sites compared to the number of individuals counted on wetland dominated sites. Furthermore, if the number of wetland dominated sites are under-represented due to the underlying data collection methods mentioned, than there are not enough wetland sites available, with wetland species counts to offset the number of terrestrial dominated sites which these wetland species are counted in. As a result, RHU scores for terrestrial habitat will be higher than wetland habitat RHU scores. Therefore, the habitat classification approach adopted in this study means that RHU can be limited if species' use of small patches of preferred habitat within a landscape matrix is important. Count data from surveys targeted towards wetlands such as the UK Waterways Breeding Bird Survey (Harris

et al., 2019), Waterfowl Monitoring in Lakes in Finland (Laaksonen et al., 2019) and Spring Waterbirds Census in Belgium (Weiserbs, 2012) could be integrated to provide additional count data for wetland species on wetland dominated sites. Doing so would mean that wetland dominated sites would have higher species' counts relative to the species' counts in terrestrial dominated sites that contain patches of wetland habitat. A unit increase in the number of wetland sites increases the counts for wetland species. This in turn would offset species' counts in terrestrial dominated sites that contain wetland patches, thereby resulting in higher RHU scores for wetland habitat and lower scores for terrestrial habitats.

We also find that 21 out of 149 species reported as only associated with terrestrial habitats have mean RHUs ≥ 1 for wetland habitat, with nine of these having higher mean RHUs for wetland habitat compared to their mean RHUs for some of their associated terrestrial habitats. This further suggests that species' habitat use at a finer spatial scale has an impact on how well RHU and literature-based classification reflect one another. Our definition of wetland habitat in this study includes inland wetlands such as marshes and peat bogs. Although these habitat types are characteristically water-logged areas, they also contain vegetation in the form of herbaceous or woody plants, dwarf shrubs, sedges, willows, mosses or scattered trees, which are also found in terrestrial habitats (Copernicus Land Monitoring Service, 2012). Therefore, it is unsurprising that some species reported as only being associated with terrestrial habitats may have mean RHUs ≥ 1 for wetlands, if they are counted in wetland sites that contain similar vegetation to terrestrial habitats. Similarly, the Roscher et al. (2015) database used in this study does not report that *Himantopus himantopus* (Black-winged stilt) is associated with farmland but analyses of relative abundance across habitats from PECBMS data identifies a mean RHU of 4.058 for farmland. Similarly, *Luscinia luscinia* (Thrush nightingale) is not reported as associated with urban habitat, yet has an RHU of 1.579 for it. This further suggests that the approach used in this study to classify sites by the dominant habitat type means that RHU and literature-derived classifications are less likely to reflect one another. In particular when species' specific ecology is important, as is the case with these two species for example. Other literature sources reporting on specific habitat use of these species suggest that Black-winged stilt is found on irrigated farmland or wet pastures (BirdLife International, 2021), and Thrush nightingale can be found in urban parks and gardens (Csörgő et al., 2018). Classifying sites by the dominant habitat means that species' association with and degree of specialization for habitats is interpreted in a wider landscape context. This highlights a weakness in RHU in that it identifies associations with habitats that it is not necessarily associated with.

Interestingly, the pattern of difference in mean RHUs between species grouped by their reported degree of specialization for semi-natural habitat deviate from those for the other habitats. One explanation for this is that semi-natural habitat encompasses a range of CLC Level three habitats (see Table A1), where there is greater variation within this habitat type compared to the variation within the other four habitats. Therefore, our interpretation of results for semi-natural should be treated with caution, as species' association with some habitats grouped under semi-natural are stronger than their associations with other habitats grouped under semi-natural, thereby producing results that do not follow the same pattern as other habitats. We recommend that exploration of the RHU metric for this varied habitat type should consider calculating species' RHUs for each CLC Level three habitat separately.

Variation in detectability could also introduce bias to species' RHU scores. In such cases, reduced detectability in closed habitats (Johnston et al., 2014) such as forest and urban could lead to lower counts in, and thus lower RHU scores for, those habitats. In turn, this would under-estimate the extent of their associations with closed habitats and over-estimate their associations with more open habitats (*e.g.,* farmland and semi-natural) (Larsen et al., 2011). This issue is most likely to arise for generalist species that are relatively evenly distributed across a range of habitats. However, the potential influence of varying detectability on the assessment of a species' association and specialization will decrease as that species' specialization increases. Even if a species is specialized to a closed habitat,

the variation in RHU scores between habitats will become more pronounced as counts become increasingly skewed towards the closed habitat. Detectability is therefore less likely to impact specialist species, which is an important factor to consider if the RHU approach is used to identify habitat specialists that will in turn advise conservation management.

There are also limitations that come with relying on the categorical, literature-based approach. For example, static, categorical classifications which are based on small-scale field studies, observations or expert-opinion simply group species into those that are associated or not associated with a habitat and whether those associated are specialists or generalists. This fails to account for variation between species in the extent of their association with or specialization for a habitat. Although there are specific limitations with RHU, overall it is more robust than categorical-based classifications as it is a quantitative method that is based on the most widely available data, can be calculated at any temporal or spatial scale, and can differentiate species based on the extent of their association with or degree of specialization for a given habitat. Within the time frame of this study, species associated with and more specialized to a given habitat do not show large temporal variation in their RHU scores for that habitat over time. Furthermore, species that are less specialized to a habitat have higher temporal variation in RHU scores due to their capacity to exploit different habitat types for required resources. By comparison, more specialized species are limited in the number of habitats they are capable of using, as the environmental conditions and resources they require for foraging or breeding will be found in a single or limited number of habitats. These results give us further confidence in using RHU to classify species as associated with or more specialized to a given habitat as these species are unlikely to vary in their habitat associations over time.

5. Conclusion

We find that quantitative, RHU-based assessments of species' association with and degree of specialization for a given habitat are broadly similar to literature-based categorical classifications. We also find that RHU scores for given habitat are relatively stable in time, particularly if associated with and more specialized to that habitat. While there is general consistency between these two methods, RHU offers a more robust approach by quantifying the extent of species' association with each habitat in which it is recorded. Calculating RHU scores annually allows classifications for association and specialization to also be

updated if necessary. We therefore recommend that the RHU metric should be considered further as a useful tool to identify and classify species by their habitat associations and degree of specialization. Doing so would support conservation management strategies to protect habitat specialists and their habitats, and thus support national and international progress towards reaching biodiversity targets.

6. Authors' contributions

E.O.R. and S.J.B devised the study. E.O.R. analysed the data and wrote the paper. S.J.B. provided guidance and wrote parts of the paper. R.D.G provided feedback and advice throughout the formation of the paper and commented on the manuscript throughout. All other authors checked and analysed national scheme's data and commented on the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.
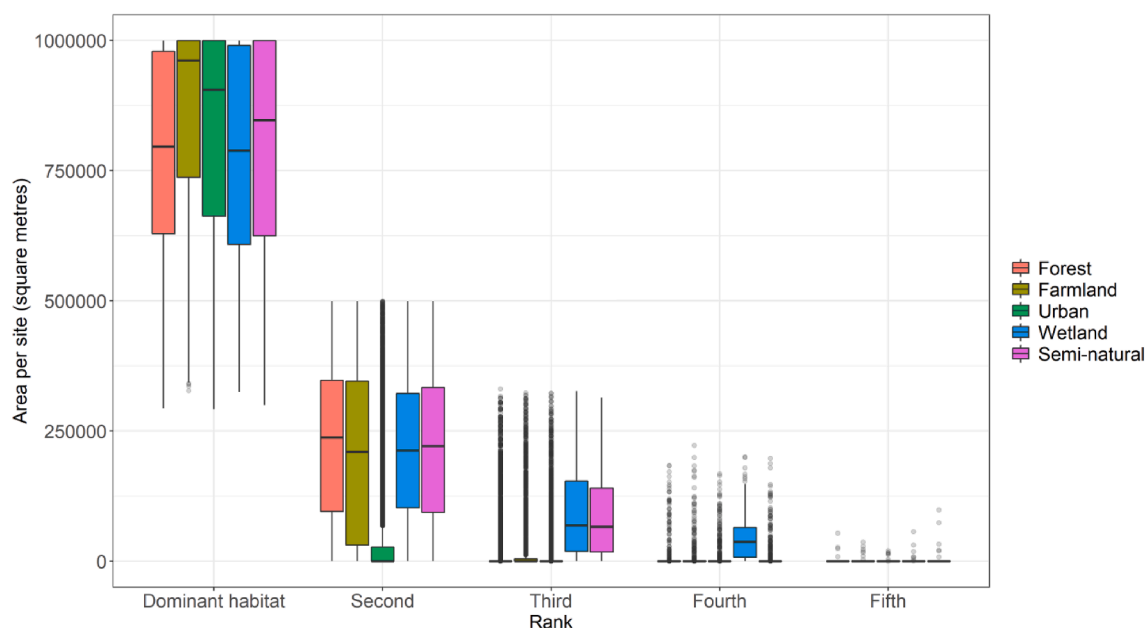
Appendix A

Fig. A1. Area (square metres) for habitats ranked as either the dominant habitat, second, third, fourth or fifth largest area based on total area of the habitat in each site. Habitats are grouped according to their rank based on total area per site.

Table A1

Corine Land Cover 2012 Levels 1 – 3 with habitat category assigned to each Level 3 habitat.

Assigned habitat category	Level 1	Level 2	Level 3
Urban	Artificial surfaces	Urban fabric	Continuous urban fabric Discontinuous urban fabric
		Industrial, commercial and transport units	Industrial or commercial units Road and rail networks and associated land Port areas Airports
		Mine, dump and construction sites	Mineral extraction sites Dump sites Construction sites
		Artificial, non-agricultural vegetated areas	Green urban areas Sport and leisure facilities
Farmland	Agricultural areas	Arable land	Non-irrigated arable land Permanently irrigated land Rice fields
		Permanent crops	Vineyards Fruit trees and berry plantations Olive groves
		Pastures	Pastures
		Heterogeneous agricultural areas	Annual crops associated with permanent crops Complex cultivation patterns Land principally occupied by agriculture, with significant areas of natural vegetation Agro-forestry areas
Forest	Forest and semi natural areas	Forests	Broad-leaved forest Coniferous forest Mixed forest
Semi-natural	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Natural grasslands Moors and heathland Sclerophyllous vegetation Transitional woodland-shrub
		Open spaces with little or no vegetation	Beaches, dunes, sands Bare rocks Sparsely vegetated areas Burnt areas Glaciers and perpetual snow
Wetland	Wetlands	Inland wetlands	Inland marshes Peat bogs
		Maritime wetlands	Salt marshes Salines Intertidal flats
	Water bodies	Inland waters	Water courses Water bodies

Table A3

Kruskal-Wallis and post-hoc Dunn's tests examining the influence of reported degree of habitat specialization on RHU. Separate models were run for each habitat, with species grouped according to whether they were reported in the species-habitat linkage database (Roscher et al., 2015) as being only associated with that habitat, associated with that habitat and one other, associated with that habitat and two others, or not reported as associated with that habitat.

Focal habitat					
Reported degree of habitat specialization	Forest	Farmland	Urban	Wetland	Semi-natural
	chi^2 = 106.65 df = 3 p < 0.001	chi^2 = 68.604 df = 3 p < 0.001	chi^2 = 40.728 df = 3 p < 0.001	chi^2 = 118.66 df = 3 p < 0.001	chi^2 = 60.591 df = 3 p < 0.001
Focal habitat only vs Focal plus one	Z = 2.918 p = 0.002	Z = 1.345 p = 0.089	Z = 1.009 p = 0.156	Z = 2.392 p = 0.008	Z = 2.435 p = 0.007
Focal habitat only vs Focal plus two	Z = 3.928 p < 0.001	Z = 3.380 p < 0.001	Z = 0.929 p = 0.176	Z = 0.865 p = 0.194	Z = 0.779 p = 0.218
Focal habitat only vs No focal habitat use	Z = 9.522 p < 0.001	Z = 4.477 p < 0.001	Z = 2.660 p = 0.004	Z = 9.106 p < 0.001	Z = 5.533 p < 0.001
Focal plus one vs Focal plus two	Z = 1.773 p = 0.038	Z = 3.650 p < 0.001	Z = -0.047 p = 0.481	Z = -0.905 p = 0.183	Z = -1.647 p = 0.05
Focal plus one vs No focal habitat use	Z = 6.370 p < 0.001	Z = 7.378 p < 0.001	Z = 5.066 p < 0.001	Z = 6.683 p < 0.001	Z = 4.865 p < 0.001
Focal plus two vs No focal habitat use	Z = 2.347 p = 0.009	Z = 1.209 p = 0.113	Z = 3.408 p < 0.001	Z = 5.237 p < 0.001	Z = 5.015 p < 0.001

Table A4

Total number of sites of each dominant habitat type at a Pan-European level.

Dominant habitat	Number of sites
Forest	5250
Farmland	10,907
Urban	2406
Wetland	1244
Semi-natural	2081

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108521.

References

BirdLife International, 2021. IUCN Red List for birds. http://www.birdlife.org (accessed 4 February 2021).

BirdLife International. Birds and biodiversity targets: what do birds tell us about progress to the Aichi Targets and requirements for the post-2020 biodiversity framework? A State of the World's Birds report 978–1 2020 BirdLife International Cambridge, UK ISBN no-912086-67-2.

Boutin, C., Jobin, B., 1998. Intensity of agricultural practices and effects on adjacent habitats. Ecol. Appl. 8, 544–557. https://doi.org/10.1890/1051-0761(1998)008 [0544:IOAPAE]2.0.CO;2.

Brlík, V., Šilarová, E., Škorpilová, J., Alonso, H., Anton, M., Aunins, A., Benkö, Z., Biver, G., Busch, M., Chodkiewicz, T., Chylarecki, P., Coombes, D., de Carli, E., del Moral, J.C., Derouaux, A., Escandell, V., Eskildsen, D.P., Fontaine, B., Foppen, R.P. B., Klvaňová, A., 2021. Long-term and large-scale multispecies dataset tracking

population changes of common European breeding birds. Sci. Data 8, 21. https://doi.org/10.6084/m9.figshare.13240760.

Chazdon, R.L., Chao, A., Colwell, R.K., Lin, S.-Y., Norden, N., Letcher, S.G., Clark, D.B., Finegan, B., Arroyo, J.P., 2011. A novel statistical method for classifying habitat generalists and specialists. Ecology 92 (6), 1332–1343. https://doi.org/10.1890/10-1345.1.

Copernicus Land Monitoring Service., 2012. Corine Land Cover 2012. https://land.copernicus.eu/pan-european/corine-land-cover/ (accessed 30 November 2018).

Csörgő, T., Fehérvári, P., Karcza, Z., Ócsai, P., Harnos, A., 2018. Exploratory analyses of migration timing and morphometrics of the Thrush Nightingale (Luscinia luscinia). Ornis Hung. 26, 149–170. https://doi.org/10.1515/orhu-2016-0019.

Devictor, V., Julliard, R., Jiguet, F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117 (4), 507–514. https://doi.org/10.1111/j.0030-1299.2008.16215.x.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010. Defining and measuring ecological specialization. J. Appl. Ecol. 47, 15–25. https://doi.org/10.1111/j.1365-2664.2009.01744.x.

Dinno, A., 2017. Dunn's Test of Multiple Comparisons Using Rank Sums. R package version 1.3.5.

EEA, 2012. Streamlining European biodiversity indicators 2020: Building a future on lessons learnt from the SEBI 2010 process. EEA Technical report No 11/2012. Copenhagen, European Environment Agency. https://www.eea.europa.eu/ (accessed 1 October 2020).

Eskildsen, A., Larsen, J., Heldbjerg, H., 2013. Use of an objective indicator species selection method shows decline in bird populations in Danish habitats. Dansk Orn. Foren. Tidsskr. 107, 191–207.

Fraixedas, Sara, Lindén, Andreas, Piha, Markus, Cabeza, Mar, Gregory, Richard, Lehikoinen, Aleksi, 2020. A state-of-the-art review on birds as indicators of biodiversity: advances, challenges, and future directions. Ecol. Indic. 118, 106728. https://doi.org/10.1016/j.ecolind.2020.106728.

Fridley, J.D., Vandermast, D.B., Kuppinger, D.M., Manthey, M., Peet, R.K., 2007. Co-occurrence based assessment of habitat generalists and specialists: a new approach for the measurement of niche width. J. Ecol. 95 (4), 707–722. https://doi.org/10.1111/j.1365-2745.2007.01236.x.

Gamero, Anna, Brotons, Lluís, Brunner, Ariel, Foppen, Ruud, Fornasari, Lorenzo, Gregory, Richard D., Herrando, Sergi, Horák, David, Jiguet, Frédéric, Kmecl, Primož, Lehikoinen, Aleksi, Lindström, Åke, Paquet, Jean-Yves, Reif, Jiří, Sirkiä, Päivi M., Škorpilová, Jana, Strien, Arco, Szép, Tibor, Telenský, Tomáš, Teufelbauer, Norbert, Trautmann, Sven, Turnhout, Chris A.M., Vermouzek, Zdeněk, Vikstrøm, Thomas, Voříšek, Petr, 2017. Tracking progress toward eu biodiversity strategy targets: EU policy effects in preserving its common farmland birds. Conserv. Lett. 10 (4), 395–402. https://doi.org/10.1111/conl.2017.10.issue-410.1111/conl.12292.

Gove, B., Power, S.A., Buckley, G.P., Ghazoul, J., 2007. Effects of herbicide spray drift and fertilizer overspread on selected species of woodland ground flora: comparison between short-term and long-term impact assessments and field surveys: herbicide and fertilizer impacts on woodland plants. J. Appl. Ecol. 44, 374–384. https://doi.org/10.1111/j.1365-2664.2007.01261.x.

Gregory, R.D., Škorpilová, J., Voříšek, P., Butler, S., 2019. An analysis of trends, uncertainty and species selection shows contrasting trends of widespread forest and farmland birds in Europe. Ecol. Indic. 103, 676–687. https://doi.org/10.1016/j.ecolind.2019.04.064.

Gregory, Richard D, van Strien, Arco, Vorisek, Petr, Gmelig Meyling, Adriaan W, Noble, David G, Foppen, Ruud P.B, Gibbons, David W, 2005. Developing indicators for European birds. Philos. Trans. R. Soc. B Biol. Sci. 360 (1454), 269–288. https://doi.org/10.1098/rstb.2004.1602.

Hagemeijer, E.J.M., Blair, M.J. (Ed.), 1997. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T and A D Poyser, London.

Handbook of the Birds of the World and BirdLife International, 2020. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. Version 5. http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v5_Dec20.zip. (accessed 17 March 2021).

Harris, S.J., Massimino, D., Eaton, M.A., Gillings, S., Noble, D.G., Balmer, D.E., Pearce-Higgins, J.W. & Woodcock, P., 2019. The Breeding Bird Survey. BTO Research Report 717. British Trust for Ornithology, Thetford.

Hayward, Matt W., O'Brien, John, Hofmeyr, Markus, Kerley, Graham I.H., 2006. Prey preferences of the african wild dog lycaon pictus (canidae: carnivora): ecological requirements for conservation. J. Mammal. 87 (6), 1122–1131. https://doi.org/10.1644/05-MAMM-A-304R2.1.

Herrando, S., Brotons, L., Anton, M., Páramo, F., Villero, D., Titeux, N., Quesada, J., Stefanescu, C., 2016. Assessing impacts of land abandonment on Mediterranean biodiversity using indicators based on bird and butterfly monitoring data. Environment 43 (1), 69–78. https://doi.org/10.1017/S0376892915000260.

Jacobs, J., 1974. Quantitative measurement of food selection. Oecologia 14 (4), 413–417. https://doi.org/10.1007/BF00384581.

Johnston, A., Newson, S.E., Risely, K., Musgrove, A.J., Massimino, D., Baillie, S.R., Pearce-Higgins, J.W., 2014. Species traits explain variation in detectability of UK birds. Bird Study 61 (3), 340–350. https://doi.org/10.1080/00063657.2014.941787.

Julliard, Romain, Clavel, Joanne, Devictor, Vincent, Jiguet, Frédéric, Couvet, Denis, 2006. Spatial segregation of specialists and generalists in bird communities. Ecol. Lett. 9 (11), 1237–1244. https://doi.org/10.1111/j.1461-0248.2006.00977.x.

Kirk, David Anthony, Park, Allysia C., Smith, Adam C., Howes, Briar J., Prouse, Brigid K., Kyssa, Naschelly G., Fairhurst, Elizabeth N., Prior, Kent A., 2018. Our use, misuse, and abandonment of a concept: whither habitat? Ecol. Evol. 8 (8), 4197–4208. https://doi.org/10.1002/ece3.2018.8.issue-810.1002/ece3.3812.

Laaksonen, T., Lehikoinen, A., Pöysä, H., Sirkiä, P., Ikonen, K., 2019. Inland waterfowl population trends 1986–2018. – Linnut-vuosikirja 2018: 46–55.

Larsen, Jørn Lennart, Heldbjerg, Henning, Eskildsen, Anne, 2011. Improving national habitat specific biodiversity indicators using relative habitat use for common birds. Ecol. Indic. 11 (5), 1459–1466. https://doi.org/10.1016/j.ecolind.2011.03.023.

Levins, R., 1968. Evolution in Changing Environments. Princeton University Press, Princeton, NJ.

Lumbierres, M., Dahal, P.R., Di Marco, M., Butchart, S.H.M., Donald, P.F. and Rondinini, C., 2021. Translating habitat class to land cover to map area of habitat of terrestrial vertebrates. Biol. Conserv. Accepted Author Manuscript. https://doi.org/10.1111/cobi.13851.

Maes, J., Teller, A., Erhard, M., Liquete, C., Braat, L., Berry, P., Egoh, B., Puydarrieux, P., Fiorina, C., Santos, F., Paracchini, M. L., Keune, H, Wittmer, H., Hauck, J., Fiala, I., Verburg, P. H., Condé, S., Schägner, J. P., San Miguel, J., Estreguil, C., Ostermann, O., Barredo, J. I., Pereira, H. M., Stott, A., Laporte, V., Meiner, A., Olah, B., Royo Gelabert, E., Spyropoulou, R., Petersen, J.E., Maguire, C., Zal, N., Achilleos, E., Rubin, A., Ledoux, L., Brown, C., Raes, C., Jacobs, S., Vandewalle, M., Connor, D., Bidoglio, G., 2013. Mapping and Assessment of Ecosystems and their Services. An analytical framework for ecosystem assessments under action 5 of the EU biodiversity strategy to 2020. Publications office of the European Union, Luxembourg. https://doi.org/10.2779/12398.

Morelli, F., Benedetti, Y., Møller, A.P., Fuller, R.A., 2019. Measuring avian specialization. Ecol. Evol. 9, 8378–8386. https://doi.org/10.1002/ece3.5419.

Mullarney, K., Svensson, L., Zetterström, D., 2009. Collins Bird Guide. The most complete Guide to the Birds of Britain and Europe. (Second edition).

Niemeijer, David, de Groot, Rudolf S., 2008. A conceptual framework for selecting environmental indicator sets. Ecol. Indic. 8 (1), 14–25. https://doi.org/10.1016/j.ecolind.2006.11.012.

Pereira, H., Davidcooper, H., 2006. Towards the global monitoring of biodiversity change. Trends Ecol. Evol. 21 (3), 123–129. https://doi.org/10.1016/j.tree.2005.10.015.

Petraitis, P.S., 1979. Likelihood measures of niche breadth and overlap. Ecology 60, 703–710. https://doi.org/10.2307/1936607.

R Core Team., 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Redhead, J.W., Fox, R., Brereton, T., Oliver, T.H., 2016. Assessing species' habitat associations from occurrence records, standardised monitoring data and expert opinion: a test with British butterflies. Ecol. Indic. 62, 271–278. https://doi.org/10.1016/j.ecolind.2015.11.004.

Reid, W.V., Mooney, H.A., Cropper, A., Capistrano, D., Carpenter, S.R., Chopra, K., Dasgupta, P., Dietz, T., Duraiappah, A.K., Hassan, R., Kasperson, R., Leemans, R., May, R.M., McMichael, A.J., Pingali, P., Samper, C., Scholes, R., Watson, R.T., Zakri, A.H., Shidong, Z., Ash, N.J., Bennett, E., Kumar, P., Lee, M.J., Raudsepp-Hearne, C., Simons, H., Thonell, J., Zurek, M.B., 2005. Ecosystems and human well-being - Synthesis: A Report of the Millennium Ecosystem Assessment. Island Press, Washington D.C.

Reif, Jiří, Storch, David, Voříšek, Petr, Šťastný, Karel, Bejček, Vladimír, 2008. Bird-habitat associations predict population trends in central European forest and farmland birds. Biodivers. Conserv. 17 (13), 3307–3319. https://doi.org/10.1007/s10531-008-9430-4.

Reif, Jiří, Jiguet, Frédéric, Šťastný, Karel, 2010. Habitat specialization of birds in the Czech Republic: comparison of objective measures with expert opinion. Bird Study 57 (2), 197–212. https://doi.org/10.1080/00063650903477046.

Renwick, A.R., Johnston, A., Joys, A., Newson, S.E., Noble, D.G., Pearce-Higgins, J.W., 2012. Composite bird indicators robust to variation in species selection and habitat specificity. Ecol. Indic. 18, 200–207. https://doi.org/10.1016/j.ecolind.2011.11.008.

Rivas-Salvador, J., Horák, D., Reif, J., 2019. Spatial patterns in habitat specialization of European bird communities. Ecol. Indic. 105, 57–69. https://doi.org/10.1016/j.ecolind.2019.05.063.

[https://www.eea.europa.eu/data-and-maps/data/linkages-of-species-and-habitat] Roscher, S., Condé, S., Bailly Maitre, J., 2015. Final database on linkages between species/habitat types and broad ecosystems. ETC/BD report to the EEA. Retrieved from: https://www.eea.europa.eu/legal/copyright.

Smart, Simon M, Thompson, Ken, Marrs, Robert H, Le Duc, Mike G, Maskell, Lindsay C, Firbank, Leslie G, 2006. Biotic homogenization and changes in species diversity across human-modified ecosystems. Proc. R. Soc. B Biol. Sci. 273 (1601), 2659–2665. https://doi.org/10.1098/rspb.2006.3630.

Thogmartin, Wayne E., Knutson, Melinda G., 2007. Scaling local species-habitat relations to the larger landscape with a hierarchical spatial count model. Landsc. Ecol. 22 (1), 61–75. https://doi.org/10.1007/s10980-006-9005-2.

Tucker, G.M., Evans, M.I., 1997. Habitats for birds in Europe: a conservation strategy for the wider environment. BirdLife Conserv. Ser. 6.

Wade, Amy S.I., Barov, Boris, Burfield, Ian J., Gregory, Richard D., Norris, Ken, Butler, Simon J., Farwig, Nina, 2013. Quantifying the detrimental impacts of land-use and management change on European forest bird populations. PLoS ONE 8 (5), e64552. https://doi.org/10.1371/journal.pone.0064552.

Wade, Amy S.I., Barov, Boris, Burfield, Ian J., Gregory, Richard D., Norris, Ken, Vorisek, Petr, Wu, Taoyang, Butler, Simon J., Bersier, Louis-Felix, 2014. A Niche-based framework to assess current monitoring of european forest birds and guide indicator species' selection. PLoS ONE. 9 (5), e97217. https://doi.org/10.1371/journal.pone.0097217.

Walpole M, Almond RE, Besançon C, Butchart, S.H., 2009. Ecology. Tracking progress toward the 2010 biodiversity target and beyond. Science (New York, N.Y.). 325, 1503-1504. https://doi.org/10.1126/science.1175466.

Weiserbs, A., 2012. Suivi printanier des populations d'oiseaux d'eau communs en région de bruxelles-capitale. Aves 49 (1), 23–28.