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Breeding bird species diversity across gradients of land use from forest to agriculture in Europe

Matti J. Koivula[1,2]*, Dan E. Chamberlain[3], Robert J. Fuller[4], Stephen C. F. Palmer[5], Attila Bankovics[6], Fintan Bracken[7,8], Tom Bolger[7], Eduardo de Juana[9], Marc Montadert[10], Renato Neves[11], Rui Rufino[11], Angel Sallent[9], Luís Lopes da Silva[11], Pedro J. Leitão[12,13], Manfred Steffen[14] and Allan D. Watt[15]

1 School of Forest Sciences, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland

2 Department of Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland

3 Department of Life Sciences and Systems Biology, University of Turin, 10123, Turin, Italy

4 British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

5 Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, UK

6 Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13., Hungary

7 School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland

8 University of Limerick, Limerick, Ireland

9 Departamento de Zoología y Antropología Física, Facultad de Biología, Planta 9, Universidad Complutense de Madrid 28040, Madrid, Spain

10 Les Granges Michel, 25300 Les Verrières de Joux, France

11 Mae D'agua, Consultoria Tecnica Em Areas De Interesse Natural, Ldt., Portugal

12 Department of Landscape Ecology and Environmental Systems Analysis, Technische Universität Braunschweig, Langer Kamp 19c, 38106 Braunschweig, Germany

13 Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

14 Hinterbergweg 8a, 4900 Langenthal/BE, Switzerland

15 Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian, EH26 0QB, UK

* Corresponding author: matti.koivula@uef.fi

Running title: Bird species richness and diversity across forest-agricultural land gradients

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Abstract

Loss, fragmentation and decreasing quality of habitats have been proposed as major threats to biodiversity world-wide, but relatively little is known about biodiversity responses to multiple pressures, particularly at very large spatial scales. We evaluated the relative contributions of four landscape variables (habitat cover, diversity, fragmentation and productivity) in determining different components of avian diversity across Europe. We sampled breeding birds in multiple 1-km^2 landscapes, from high forest cover to intensive agricultural land, in eight countries during 2001−02. We predicted that the total diversity would peak at intermediate levels of forest cover and fragmentation, and respond positively to increasing habitat diversity and productivity; forest and open-habitat specialists would show threshold conditions along gradients of forest cover and fragmentation, and respond positively to increasing habitat diversity and productivity; resident species would be more strongly impacted by forest cover and fragmentation than migratory species; and generalists and urban species would show weak responses. Measures of total diversity did not peak at intermediate levels of forest cover or fragmentation. Rarefaction-standardized species richness decreased marginally and linearly with increasing forest cover and increased non-linearly with productivity, whereas all measures increased linearly with increasing fragmentation and landscape diversity. Forest and open-habitat specialists responded approximately linearly to forest cover and also weakly to habitat diversity, fragmentation and productivity. Generalists and urban species responded weakly to the landscape variables, but some groups responded non-linearly to productivity and marginally to habitat diversity. Resident species were not consistently more sensitive than migratory species to any of the landscape variables. These findings are relevant to landscapes with relatively long histories of human land-use, and they highlight that habitat loss, fragmentation and habitat-type diversity must all be considered in land-use planning and landscape modeling of avian communities.

1. Introduction

Declines in biodiversity are occurring in many parts of the world as a result of the degradation, loss and fragmentation of habitat through human activities (e.g., Sodhi and Ehrlich 2010, Newbold et al. 2015). Policy tools to halt this negative trend include, for example, international agreements (such as the European Union’s Biodiversity Strategy 2020 and the Convention on

Biological Diversity Aichi Biodiversity Targets), establishment of reserves, and legislation on conservation and land use. The full inclusion of these agreements and tools into management, however, requires research on species responses to different forms of anthropogenic land use, such as agriculture or forestry.

Human land use affects the amount, spatial configuration, structural heterogeneity and productivity of habitat, and these may all determine biodiversity from the spatial scales of patches to landscapes (see below). By “patches” we refer to relatively uniform areas of a given habitat type and successional stage of vegetation, up to a few hectares in size. By “landscapes”, on the other hand, we refer to areas that consist of multiple patches and are at least several tens of hectares in size. The negative effect of habitat loss is predicted by the classical theory of the species-area relationship (Schoener 1976), which is supported by abundant empirical evidence (Fahrig 2003). At a general level, this relationship is widely accepted, but sometimes habitat loss has impacted biodiversity non-linearly, characterized by threshold responses (e.g., Huggett 2005). These thresholds have commonly been reported at about 10−30% habitat cover (Swift and Hannon 2010), but they vary notably. For example, Betts et al. (2010) found species-specific canopy-cover thresholds to occur between 1.4% and 24.6%, below which bird occurrence declined markedly. Other studies suggest higher thresholds: Estavillo et al. (2013) studied landscapes with varying degrees of forest fragmentation and detected an abrupt decline in species richness of closed-forest mammals at or below 30% forest cover, and Martensen et al. (2012) found a threshold of drastic avian richness decrease at 30−50% cover in Atlantic forests of Brazil. However, not all studies have reported such thresholds (e.g., Villard et al. 1999, Mikusiński and Angelstam 2004).

Thresholds suggest that habitat loss alone may not be responsible for changes in the abundance and occurrence of species. The spatial configuration of habitat – commonly referred to as fragmentation, which includes the division of formerly contiguous habitat and increases in inter-patch distances – may also play a role, particularly if the amount of habitat subject to fragmentation is small (Andrén 1994). The logic underlying the negative impact of fragmentation lies in the idea that the persistence of patchy populations requires dispersal between habitat patches (Hanski 2005). Even for relatively well-dispersing taxa, such as many birds, movements between patches become increasingly difficult with increasing fragmentation (Enoksson et al. 1995, Swift and Hannon 2010). A commonly accepted view is that habitat loss and fragmentation act in concert, and their effects are therefore difficult to distinguish in real-life situations (e.g., Fahrig 2003, 2017, Didham et al. 2012). Indeed, McGarigal and McComb (1995), Trzcinski et al. (1999) and Villard et al. (1999) showed that both forest cover and configuration were good predictors of the occupancy and abundance of breeding forest birds.

The niche theory (Hutchinson 1957) provides yet another explanation for variation in biodiversity. Increasing structural heterogeneity potentially reflects a greater variety of habitats, i.e. more niches, which in turn may allow more species to occur in the same general area. Many studies have confirmed the positive link between habitat heterogeneity and species diversity (e.g., Raivio and Haila 1990, Böhning-Gaese 1997, Pino et al. 2000, Luoto et al. 2004, Gil-Tena et al. 2007). Accordingly, loss of structural heterogeneity has led to drastic declines of biodiversity in both agricultural (Benton et al. 2003) and forested landscapes (Gauthier et al. 2015).

Biodiversity may also be positively associated with productivity (Tilman 1980, 1999). Solar energy and water availability limit plant biomass and diversity, and they, in turn, will determine herbivore and, subsequently, predator biomass and diversity (Huston 1994). This productivity-richness relationship may be hump-shaped (Ricklefs and Schluter 1993). However, many studies have reported linear relationships, but these discrepancies may result from variation in spatial scale among studies (Chase and Leibold 2002). Thus, at a local scale, a hump-shaped curve may be expected, whereas across landscapes or regions, a linear response may be more common (Chase and Leibold 2002). This is because, at landscape or regional scales, species compositions tend to become increasingly different between patches with increasing productivity.

Species traits determine biological responses to environmental variation and change. For instance, habitat specialists may be more severely impacted than generalists by loss and fragmentation of habitat (Schmiegelow and Mönkkönen 2002, Virkkala and Rajasärkkä 2006; but see Fahrig 2017), the latter being expected to be more adaptable to a range of conditions, including anthropogenic impacts. Similarly, urban species tend to be generalists in terms of niche position, though urban communities are typically comprised of species from a range of natural habitat types (Evans et al. 2010). Furthermore, resident species may be more sensitive than migratory species in this respect (Enoksson et al. 1995, Roberge and Angelstam 2006). This is because the movements of resident species are often more constrained than those of migratory species (Desrochers et al. 1999).

The majority of biological evidence that guides current land use is based on experiments or *ad hoc* comparisons conducted between patches of habitat rather than at the landscape level (cf. Koivula et al. 2014). The latter types of studies are urgently needed because certain biological phenomena cannot be fully explored at the patch level. These include responses of species assemblages that usually change gradually between patches of different habitat types, land-use impacts on species with home ranges covering multiple patches of sometimes different site types, or responses of species to landscape-level habitat use.

One approach to understanding implications of landscape changes is to examine biological communities across gradients of land use (e.g., Matson 1990, McDonnell and Pickett 1990, Blair 1996, 1999, O'Connell et al. 2000, Coppedge et al. 2001, Ribera et al. 2001, Sousa et al. 2004, Vanbergen et al. 2005). If constructed in a consistent manner, gradients can provide insights into the generality of responses of communities to environmental change. Such an approach is used in this paper to assess how the richness and diversity of breeding birds vary across gradients of land use in eight European countries. These gradients represent shifts from continuous forest at one extreme, through mosaics of forest and agricultural land, to a dominance of agricultural land at the other extreme. Such complete gradients of habitat cover have commonly produced intermediate richness peaks in abundance and richness of birds (Jokimäki and Suhonen 1993, Andrén 1994, Cushman and McGarigal 2003, Desrochers et al. 2011).

In the present paper, we attempt to identify the key landscape variables that drive bird species richness and diversity across gradients of forest cover using a unique data set based on standardized sampling methods over a large geographic area, from boreal to Mediterranean regions. More specifically, we present an analysis of the relative contributions of cover and fragmentation of forests, and structural diversity and productivity of landscapes on the species richness of bird communities. Based on research summarized above, we made the following predictions:

1. The total avian diversity (i.e., of all species) should peak at intermediate levels of forest cover and fragmentation, and should be positively associated with increases in habitat diversity and productivity.

2. The diversity of forest-associated species should show a threshold for a decline within the range of 10−50% of forest cover (e.g., Swift and Hannon 2010, Martensen et al. 2012), and below this threshold, fragmentation should become increasingly important. This richness measure should also increase with increasing diversity of forests, and productivity.

3. The diversity of open-habitat species should decline in the range 50−90% of forest cover (compare prediction #2) and with decreasing forest fragmentation, as – in the present study context – these broadly correspond to higher proportions and continuity of open habitats. The diversity of open-habitat species should also increase with increasing diversity of open habitats, and productivity.

4. Resident species should show stronger responses to forest cover and fragmentation than migratory species.

5. Species that commonly breed in both forests and open habitats (hereafter “generalists”), or in residential and industrial areas (hereafter “urban species”), should show no strong trends along the gradient.

2. Material and methods

2.1. Study design and field methods

We conducted the study in eight European countries: Finland, France, Hungary, Ireland, Portugal, Spain, Switzerland and the United Kingdom (UK) (Fig. 1). We selected a total of six sample sites, termed Land-use Units (LUUs), in one region of each of the eight countries. Each LUU consisted of a 1-km^2 square of differing habitat composition with respect to the relative amounts of forest cover and agricultural land, selected to be representative of the regional land use in each country (Supplementary materials, Table S1).

Within each LUU, we located 16 points on a regular 200 m × 200 m grid with the outermost points positioned 200 m from the edge. We collected bird data using point counts (Verner 1985) at each of the 16 sampling points per LUU. In each year, we made four counts at each point, each count lasting five minutes. We undertook the four counts as near to dawn as possible on separate occasions (visits) spread throughout the breeding season. In most countries, this was in the months April, May and June, but was slightly earlier in the Mediterranean countries and slightly later in Finland to account for latitudinal variation in the timing of breeding seasons. No counts were undertaken during excessively wet or windy conditions. As far as possible, the counts for individual visits were undertaken at all 16 points within an LUU on the same day. Observers varied the order in which sample points were surveyed on different visits. During each count, the observer recorded all birds seen or heard as long as they were deemed to be using the LUU (e.g., for nesting, displaying, foraging or roosting). The locations of these were recorded within 100-m radius of the point. In this paper, we use records of territorial pairs (indicated by a singing male, observed pair, chicks or nest, or alarm calling individuals) that were noted separately from birds that did not show territorial behavior. We do not believe that double counts of individuals would have biased our data as the sample unit was the LUU, and nearest count stations of adjacent LUUs were at least several hundred meters apart. Our estimations of expected species richness (see below), however, might be somewhat affected by occasional double counts of individuals of loud species within adjacent sampling points.

The survey took place over two years, 2001 and 2002. In 2001, due to habitat-identification or access issues, one LUU was not covered in Ireland, Portugal and Spain. In 2002, six LUUs were covered in each country. However, one of our landscape variables – the number of forest patches (see below) – included one Swiss LUU as an outlier (15, while others varied between 0 and 8) so samples for both years from this LUU were excluded from analysis.

2.2. Data preparation

We first determined the maximum number of pairs – recorded within 100 m from the observer – per point across the four visits per year. This is a common way of extracting data based on breeding observations that ensures that all likely breeders are counted (e.g., Sutherland 1996). After this phase, we pooled the 16 points for each LUU, thus resulting in 91 samples (2 years × 8 countries × 6 LUUs – 5 LUUs; see above). We then calculated two measures of bird diversity from these data: observed species richness (S_{obs}) and the expected number of species at given levels of abundance (S_{exp}), estimated from rarefaction, which we used to control for the potential greater likelihood of higher species richness occurring purely due to a greater number of individuals (James and Rathbun 1981). We calculated rarefaction separately for abundance levels of 20 and 50 individuals. Samples with fewer than 20 or 50 individuals, respectively, were excluded from these analyses.

To evaluate if species traits contributed to forest-cover responses of the bird community, we divided the observed bird species into eight groups based on Cramp et al. (1977-1994), and national expertise and sources (Sharrock 1987, Yeatman-Berthelot and Jarry 1995, Schmid et al. 1998, Väisänen et al. 1998, Szep et al. 2012, de Juana and Garcia 2015) (Appendix; see also Acknowledgements). For each group, we calculated S_{obs} for each LUU; due to the lower abundances, sample sizes were much reduced when considering species groups, and therefore S_{exp} was not analyzed. The grouping was based on a combination of migration strategy (resident or migratory), main breeding habitat (forested, open, general) and common occurrence in urban environments. We considered partial migrants – such as the Goldcrest (*Regulus regulus*) in Finland – migratory. Forested habitats included all forest types and their successional stages, and open habitats included dry bushy areas, meadows, pastures, and other types of agricultural land. We considered a given species urban if it commonly occupies industrial and residential areas; wooded city parks were not included. Species associated with wetlands were not common in the data and were therefore not considered. As these species traits varied among the eight countries for a given species, the classification varied accordingly. For example, the Stock Dove (*Columba oenas*) fell into resident species in the Spanish subset, but was considered migratory in that of Finland. Moreover, regarding the habitat criterion, a given species could fall into two categories, e.g., the Wood Pigeon (*Columba palumbus*) was often included in both urban and forest-associated species.

As explanatory variables for avian diversity, we used six landscape variables calculated from fused Landsat 7 ETM and IRS images with a 5-m resolution using FRAGSTATS version 3 (McGarigal et al. 2002; Supplementary materials, Table S1). For a detailed description of these data, see Watt et al. (2003). These variables were (1) forest cover (%); (2) forest diversity (Shannon-Wiener index based on % covers of forest-habitat types as distinguished in satellite images, including four types of each of broad-leaved, coniferous or mixed forest: recently cleared, very open, open and closed tree canopy); (3) open-habitat diversity (Shannon-Wiener index based on % covers of types of moor, farmland, pasture and meadow as distinguished in satellite images); (4) landscape diversity (Shannon-Wiener index based on % covers of all habitat types as distinguished in satellite images); (5) number of forest patches (n/km^2) as a measure of fragmentation; and (6) Normalized Difference Vegetation Index (NDVI; for a review see Pettorelli et al. 2011) as a surrogate of productivity. These were derived for the 1-km^2 area of each LUU, and they did not strongly correlate with each other (Spearman rho $< |0.6|$).

Fragmentation can be measured in several ways (Fahrig 2003). We used the number of forest patches that reflects the breaking apart of forests, but ignores distances between patches. We also considered all other fragmentation measures provided by FRAGSTATS, but these either correlated strongly with forest cover, landscape/forest/open-habitat diversity or NDVI (rho > |0.6|) or their distributions were highly skewed (skewness value > |3|).

2.3 Statistical analyses

To explain bird diversity patterns across the forest-agricultural land gradients, we used generalized additive models (GAM; cf. Zuur et al. 2009) with regression splines (Wood 2003). We ran the GAMs using year (2001 or 2002, to account for temporal dependence of samples) and country (the eight countries, to account for spatial dependence of measures on geographic variation) as random effects, and the six landscape variables (see above) as continuous fixed effects, subject to smoothing. Each model included only prediction-based subsets of the six landscape variables (see below). Prior to the analysis, we scaled all landscape variables to vary between 0 and 100. We did not include interaction terms due to the low numbers of repeated measures (two years) and spatial replication (six samples per country), and the ambiguity of the interpretation of smoother interactions. To avoid over-fitting we set the maximum degrees of freedom for each smooth term to 3, and gamma to 1.4 (Zuur et al. 2009). Regarding the two groups of open-habitat species, however, preliminary runs suggested over-fitting of open-habitat diversity, as the response curve was an S lying on its side (peak-low-peak-low). Therefore, we set the maximum df = 2 for open-habitat diversity in these two models. After each preliminary run, we tested the normality of residuals using Q-Q plots (e.g., Sokal and Rohlf 1995). The residuals followed a normal distribution in all cases. Hence we applied the Gaussian error distribution with identity link function for the non-integer S_{exp}, but applied the Poisson error distribution with log link function for S_{obs} as it bounds these measures to zero. After each run, we applied Moran's *I* (Moran 1950) based on model residuals and a latitude-longitude distance matrix to detect possible remaining spatial autocorrelation. There was evidence of significant negative spatial autocorrelation in the whole community measures (S_{obs}, S_{exp20} and S_{exp50}), although this was largely driven by outliers in the Portuguese data set (Supplementary materials, Table S2, Fig. S1). There was no longer significant autocorrelation when this country was omitted and models re-run. Furthermore, results were very similar to the full data set when omitting Portugal (Supplementary materials, Table S3). We therefore conclude that our model outputs were robust to spatial autocorrelation effects.

We used the following sets of landscape variables, which were linked respectively to each set of predictions:

S_{obs}, S_{exp20} and S_{exp50} = forest cover + forest fragmentation + landscape diversity + NDVI

Forest species richness = forest cover + forest fragmentation+ forest diversity + NDVI

Open-habitat species richness = forest cover + forest fragmentation + open-habitat diversity + NDVI

Generalist and urban species richness = forest cover + forest fragmentation + landscape diversity + NDVI

We performed all calculations and analyses using R 3.4.1 (R Core Team 2017) software with mgcv 1.8 (Wood 2017) and ape 4.1 (Paradis et al. 2017) packages. We report % deviance as an indicator of explained variation by each model variable, and adjusted R^2 for the coefficient of determination of the full model. We considered $p \leq 0.05$ significant, but we also note results at $p < 0.10$, which we consider marginally significant.

3. Results

3.1. Overall responses to the forest-agricultural land gradients

For the three measures of total avian diversity, variation between years did not explain any of the model deviance, whereas variation among the eight countries accounted for on average 40.9% (Table 1). The effect of forest cover was small, but marginally significant and negative for both S_{exp} measures, and the effect of number of forest patches – our surrogate for increasing fragmentation of forests – was positive and linear for all three measures, though only marginally so for S_{exp20} (Table 1). All three total diversity measures positively and linearly responded to increasing landscape diversity. Of the three measures, S_{obs} did not respond to NDVI, but S_{exp20} and marginally also S_{exp50} showed approximately concave responses (Table 1, Fig. 2). The S_{exp} measures thus increased rather steeply up to NDVI values of about 0.60−0.70, above which they reached a plateau or even slightly decreased (Table 1, Fig. 2). Due to the similarity of responses among the three measures, only S_{exp20} is shown in Fig. 2.

3.2. Responses of different species-trait groups to the forest-agricultural land gradients

For the forest and open-habitat species groups, the variable Year accounted for on average 0.3% and Country accounted for on average 27.8% of variation in species richness (Table 2).

Forest cover explained on average 9.1% of variation, whereas number of forest patches, forest or open-habitat diversity, and NDVI explained relatively little (averages 1.0%, 1.1% and 1.9%, respectively; Table 2). Forest cover was significant in all cases, its effect resulting in linear or near-linear positive (forest species) or negative responses (open-habitat species) (Fig. 3). The non-linear response of migratory open-habitat species suggests slightly intensifying declines above 30−40% forest cover.

Increasing number of forest patches was positively and linearly associated with resident forest species richness, whereas the other three habitat-specialist groups did not respond to this variable (Table 2).

Habitat diversity had no detectable effect on forest species or migratory open-habitat species, but resident open-habitat species showed a marginally significant, convex response (Table 2). As such, the curve appears difficult to interpret, and there was no general linear trend along the open-habitat diversity gradient (Spearman correlation for partial residuals: rho = −0.17, *p* = 0.103). The partial residuals, however, correlated significantly with open-habitat diversity in LUUs with low, but not in LUUs with high, open-habitat diversity (rho = −0.42 and 0.16, and *p* = 0.006 and 0.269, respectively).

NDVI affected positively and non-linearly – though only marginally – resident forest species, and negatively and linearly both groups of open-habitat species (Table 2, Fig. 4). The former increased rather steeply up to about an index value of 60−70, above which either the richness continued to increase very slowly or reached a plateau (Fig. 4).

Generalists showed varying and usually minor responses to the four landscape variables (Table 2). Country again accounted for most of the explained variation and Year had virtually no impact. Resident and migratory generalists did not significantly respond to any of the four landscape variables, except to NDVI by resident generalists: their richness increased rather steeply up to a plateau at an index value of about 0.70−0.80 (Fig. 4).

The four landscape variables were also generally rather poor predictors of the species richness of urban species (Table 2). Migratory urban species responded positively, albeit only marginally, to increasing landscape diversity, and this group also showed a concave yet marginal response to NDVI, with peak at about 0.60−0.75 (Fig. 4).

4. Discussion

4.1. Total avian diversity was strongly impacted by country, fragmentation and landscape diversity

Country was the most important determinant of avian diversity in our data and accounted for, on average, about one-third of explained variation in all 11 analyses. Comparisons between countries were beyond the scope of our analysis, but this striking variation might be explained by, for example, altitudinal variation, land-use history and its current intensity (e.g., Marzluff 2001, Eriksson et al. 2002, Vellend 2004), types of forest and farmland, and their associated structural elements (see below). Yet another possibility is solar energy associated with productivity (e.g., Hawkins et al. 2003). Unsurprisingly, country-specific average latitudes of our sampling points correlated negatively with respective growing degree days (rho = -0.51). Growing degree days did not markedly correlate with the total diversity measures, whereas they correlated rather strongly and positively with the species richness of all groups of resident species, and negatively with that of all groups of migratory species (Supplementary materials, Table S4). Thus, large-scale geographic variation, partly linked with solar energy, was notable for all species groups so that migratory species appeared most species rich in the north, whereas resident species showed the opposite tendency.

No total diversity measure was markedly affected by forest cover. Thus, our prediction #1 on intermediate diversity peaks along the forest-cover gradient was not supported. Preliminary runs with only year, country and forest cover resulted in rather clear intermediate peaks for the three total diversity measures (Supplementary materials, Table S5, Fig. S2). Different combinations of landscape variables, however, either resulted in a non-significant intermediate peak along the forest-cover gradient, or the trends remained linear, as in Fig. 2. These results suggest that consideration of forest cover alone may give misleading conclusions of its effects on the bird community, and that the apparent decline in diversity at higher levels of forest cover is in fact more closely correlated with other landscape-level variables. Several other factors may thus mediate the effect of forest cover, such as variation in gradient lengths of landscape variables, partial correlations between forest cover and the other landscape variables, or partial correlations between forest cover and unmeasured but important smaller-scale variables, such as habitat structure and land use intensity (see below). Furthermore, although we were interested in general patterns of bird diversity, it should be acknowledged that each country had a unique combination of species, and the responses of individual species in shaping the overall community response between the eight countries is likely to have also been important in causing variability in responses to the gradients considered.

All measures of total avian diversity were positively associated with increasing fragmentation and landscape diversity (prediction #1). Similarly, positive relationships between avian richness and landscape structural heterogeneity have earlier been reported by McGarigal and McComb (1995), Böhning-Gaese (1997), Rodewald and Yahner (2002), Tews et al. (2004) and Mitchell et al. (2006). High habitat diversity is a positive feature for biodiversity as long as patches remain sufficiently large for species (Schippers et al. 2015).

Our surrogate for productivity (NDVI) had strong effects on expected, but not observed, species richness, the former showing threshold conditions above which the increase rapidly evened out (prediction #1; Fig. 1). At a local level, such as within each of our eight study regions, species richness should peak at intermediate levels of productivity (Chase and Leibold 2002), and the non-linear response of expected richness partly supports this view. The difference between expected (positive response) and observed richness (no response), on the other hand, probably resulted from an increase in abundance of several species along the productivity gradient.

A positive association between productivity or energy surrogates and bird richness has earlier been reported for forest specialists in Finnish forest reserves (Honkanen et al. 2010), but to our knowledge, our study is the first to report threshold conditions for species diversity across a productivity gradient. Increasing productivity and resource biomass may result in higher habitat diversity and more trophic levels, which in turn support higher species richness through principles of niche theory (Fretwell 1987, Abrams 1995, Turner et al. 2001, Evans et al. 2006). Above the threshold, productivity continues to increase but the diversity of habitat types and other resources may not do so.

4.2. Habitat specialists responded strongly to forest cover

The species richness of forest and open-habitat specialists responded rather linearly to changes in forest cover, providing partial support for our predictions #2-3 (Fig. 3). This linearity could result from bird communities which included a continuity of species with varying home-range or local-population sizes (Haila 2002). Thus, with increasing habitat loss, species requiring large tracts of habitat would disappear first, followed by species with smaller home ranges. Moreover, forest fragmentation, habitat diversity or productivity had generally minor influence, in accord with other studies that have shown that habitat amount is a better predictor of bird abundance or distribution than its spatial configuration (McGarigal and McComb 1995, Trzcinski et al. 1999, Fahrig 2002, 2017). Our results broaden these generalizations to species richness.

Regarding the four groups of specialists, we found some support for a forest-cover threshold only for migratory open-habitat species which showed a non-linear relationship (Fig. 3; see also Supplementary materials, Fig. S2). The decline in these specialists began to accelerate at about 30−40% forest cover (Fig. 3; see also Supplementary materials, Fig. S2), a value lower than our expected predictions of ≥50% forest cover. Moreover, a preliminary analysis with only country, year and forest cover also suggested a threshold in resident forest species richness at about 30−50% forest cover (Supplementary materials, Table S5, Fig. S2), in support of our predictions #2-3. Fragmentation may be key for understanding the contrast between this result and that presented in Fig. 3. There was a non-linear relationship between forest cover and the number of forest patches: these variables correlated positively in LUUs with low (<50%) and negatively in LUUs with high (≥50%) forest cover (rho = 0.47 and −0.70, respectively). Accordingly, the richness of resident forest species correlated clearly with forest cover in low- but less markedly in high-cover samples (rho = 0.42 and 0.21, respectively), whereas the correlations with patch number were perhaps less prominent, but suggested opposite directions in low- and high-cover samples (rho = 0.24 and −0.26, respectively). Thus, fragmentation apparently impacted resident forest species when forest cover was low, supporting Andrén (1994) and Hanski (2005).

The positive effect of fragmentation on resident forest species supports Fahrig (2017) who showed that most fragmentation responses are positive, even when rare or specialized species are considered. In the present study, this pattern may be partly related to the non-linear covariation between forest cover and number of patches (see above), but also to variation in the degree of specialization. Thus, some of the forest species may be able to tolerate edge conditions in small fragments or even utilize replacement habitats. Different responses to habitat loss by strict habitat specialists and flexible habitat users may result in species turnover (e.g., Schmiegelow et al. 1997). Moreover, if the flexible habitat users increase more rapidly than the rate at which strict specialists disappear, the total richness will increase with increasing fragmentation.

Many LUUs with no or very little forest or no agricultural land frequently hosted several species specialized on these habitat categories (Fig. 3). All five LUUs with up to 1% forest cover hosted forest species, the range in richness being 2−9 species. Similarly, among the ten LUUs with at least 99% forest cover, eight hosted open-habitat species (range 1−7 species). Previously, Berg (2002) has shown that many farmland birds can be most abundant in agricultural areas that include forests. These examples suggest flexible habitat use and/or that forest-farmland edges or other minor components of landscapes support these species (e.g., Terraube et al. 2016). It is, therefore, difficult to exactly determine where focal habitat ends and matrix (*sensu* Turner et al. 2001) begins, particularly where species assemblages or communities are concerned. For example, some forest species are able to utilize gardens, rows of trees, or bushy patches (Hinsley and Bellamy 2000, Fuller et al. 2007). Some open-habitat species, on the other hand, utilize forest edges, early stages of secondary succession, or forests with sparsely distributed trees for breeding, foraging or roosting (Berg and Pärt 1994, Reino et al. 2009).

4.3. Migratory strategy, generalists and urban species, and the effect of productivity

According to our analysis, migratory strategy was not systematically linked with sensitivity to habitat loss or fragmentation, or any other landscape variable; thus, our prediction #4 was not supported. Responses to forest cover were similar between resident and migratory specialists, and migratory strategy was inconsistently linked with the other landscape variables (Table 2). Such varying responses to landscape structure might be related to the degree of specialization (see above). For example, many closed-forest specialists are also resident, whereas forest-succession generalists are often migratory (Schmiegelow et al. 1997, Schmiegelow and Mönkkönen 2002, Brotons et al. 2003, Virkkala and Rajasärkkä 2006).

In line with our prediction #5, generalists and urban species showed rather weak responses and, contrary to specialists (see above), did not respond to forest cover. These patterns may have resulted from these species being rather heterogeneous in terms of requirements for habitat, and/or from being well adapted to changes in land use (e.g., Büchi and Vuilleumier 2016). An in-depth understanding of responses to landscape structure by these species would require a species-level approach on abundances or occurrences (Betts et al. 2014), and a multiple-view consideration of specialization. In the present paper, the focus was on species diversity.

Two groups of resident species, generalists and forest species, showed threshold conditions along the productivity gradient, following the trend of total richness (Figs. 2 and 4). Migratory urban species, on the other hand, peaked at intermediate productivity, and migratory open-habitat species decreased linearly (Fig. 4). These responses might reflect richness limits set by regional avifauna, but also intensifying intra- or inter-specific interactions, such as resource competition or predation (Fretwell 1987, Abrams 1995). The negative slope of migratory open-habitat species in particular might reflect adaptations to low-competition, resource-poor environments.

4.4. Structural elements, gradient lengths, spatial scales, and species classifications

Our set of landscape measures was limited by available satellite images and software. Even where the landscape structure was similar, there could be differences in the quality of habitat (the amount and diversity of structures and processes characteristic of each habitat) for birds within patches that were ostensibly the same. Indeed, several studies have found patch characteristics to be more important than patch area (Benton et al. 2003, Heikkinen et al. 2004, Wretenberg et al. 2010, Galitsky and Lawler 2015, Humphrey et al. 2015). Potentially important factors for avian richness include those that are directly linked to fertility (such as soil type; Mittelbach et al. 2001), land-use intensity (e.g., road length, the amount of traffic, human population density, the proportion of managed and unmanaged habitat; Gnass Giese et al. 2015), historical land use, which may be particularly important for poorly-dispersing organisms (Bellemare et al. 2002, De Keersmaeker et al. 2015), and certain structural features of known importance for many specialized species, such as dead wood, very large individual trees, or certain types of micro-habitat that remained undetected in our satellite images (Götmark and Thorell 2003, Luoto et al. 2004).

Some effects may also have been missed because of a limited range of variation and “gaps” in our data. Most notably, gradients of landscape diversity and productivity may have represented only part of regional variation, although the landscapes were initially selected so as to be structurally representative for regional forest-agricultural mosaics (Watt et al. 2003). Also, our forest-cover gradient had relatively poor coverage at 25−30% and 60−80%, which may have somewhat impacted our results. Furthermore, larger spatial scales might have produced different results (Stephens et al. 2003). Multi-species studies are also sensitive to at least the selection of species traits to study, and the categorization of species. We attempted to account for the latter issue by applying country specificity in classifying species according to their breeding habitat and migratory strategy, but our approach was nevertheless a simplification. The degree of specialization to habitat conditions by the studied species (Appendix) is rather a gradient than a series of sharply-delimited categories – urban, forest or agricultural land – which may appear important in evaluations of species turnover and associated variation in responses to fragmentation. The regional species pool might have constrained such responses: the number of resident forest species, for example, was 4−8 in Finnish LUUs but was 0−4 in Hungarian LUUs. Our classification also involves subjectivity, although we used both national expertise and inventory-based literature for this (see Material and methods). Different classifications would possibly have resulted in somewhat different results, particularly if more detailed habitat associations were involved (Fuller 2012). However, increasing detail results in lower generality and frequently also sample sizes too low for analysis.

4.5. Conclusions

Landscape features determining different diversity measures of the Pan-European bird community were different from those determining the species richness of different ecological groups of birds. The former were consistently determined by the spatial configuration of forests, landscape diversity and often also by productivity, whereas species specialized to forests and open habitats were all determined by forest cover. Generalists and urban species, on the other hand, responded rather weakly to our landscape measures. These results indicate that the amount, fragmentation and structural heterogeneity of habitats, and landscape productivity, all appear important determinants of avian community structure in the sense of species of different habitat preferences and migratory strategies. These thus affect different parts of the bird community in different ways, so no single measure of landscape structure can be used to predict the whole bird community. It must also be emphasized that habitat loss and fragmentation are closely related (Fahrig 2003, 2017, Didham et al. 2012, Villard and Metzger 2014). Therefore, both need to be considered in, for example, landscape modeling and conservation planning. The present results also strongly indicate that these two do not suffice, but habitats should in addition be of good quality in terms of habitat-type diversity.

Historical, economic and climatic factors complicate the identification of landscape gradients that are exactly the same in different parts of Europe. The relative importance of different structural features may vary accordingly, and processes operating at landscape scales are expected to vary regionally according to landscape history and processes related to interspecific interactions. Moreover, as our analyses showed, bird communities vary structurally among countries, which likely affects their ability to adapt to climatic alterations, habitat loss, fragmentation and altered quality of habitat.

A gradient that more accurately reflects anthropogenic disturbance would need to sample pristine habitats. The inclusion of such sites might reveal different results to those described in this paper (cf. Zlonis and Niemi 2014). However, with a few exceptions, such habitats are rare in Europe (Aksenov et al. 1999), so the patterns described here can be considered relevant to the highly disturbed cultural landscapes that dominate most of the continent.

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Figures

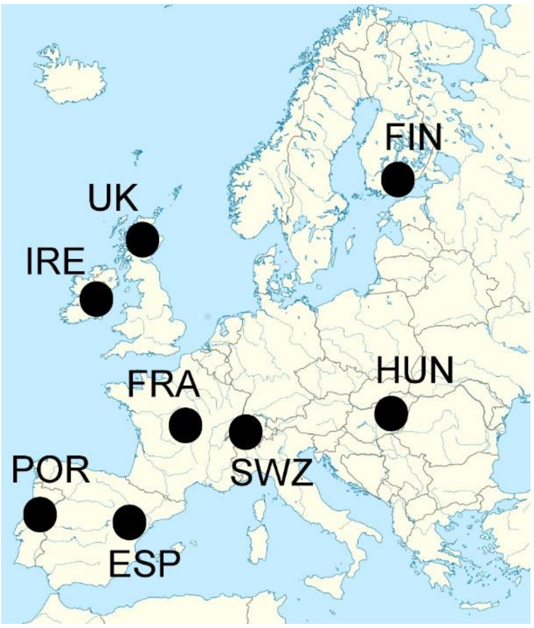

Fig. 1. The locations of eight study countries: Finland (FIN), France (FRA), Hungary (HUN), Ireland (IRE), Portugal (POR), Spain (ESP), Switzerland (SWZ) and the United Kingdom (UK). Source for the basic map: https://commons.wikimedia.org/wiki/File:Europe_laea_location_map.svg; used under the Creative Commons license CC-BY-SA-3.0. Adapted from the original map by slightly cropping, and by adding country points and abbreviations.

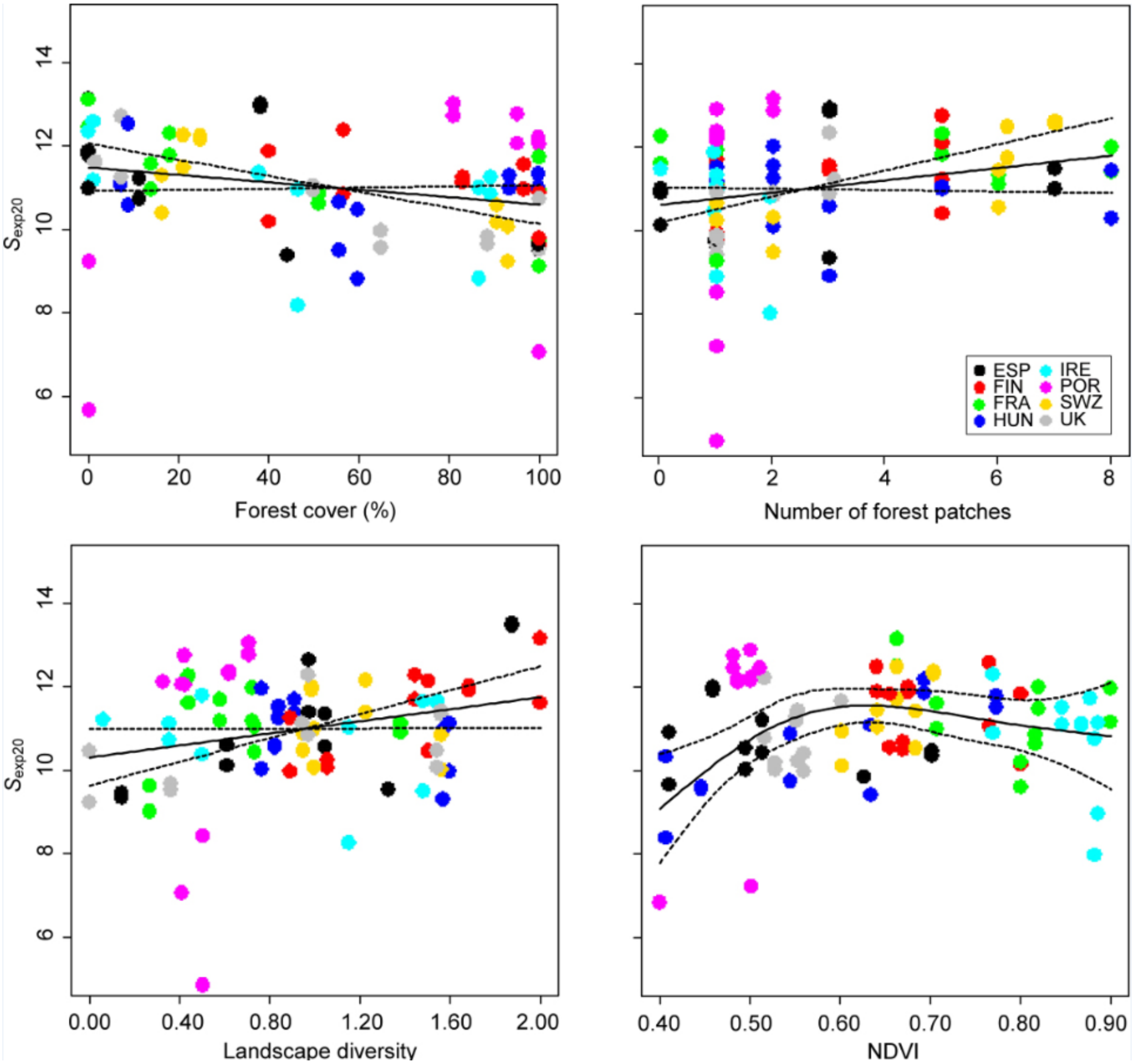

Fig. 2. GAM plots for the expected species richness for 20 individuals (S_{exp20}). For descriptions of model variables, see Material and methods; for statistical significance, see Table 1. Residuals for each country are shown with different colors (see legend box); solid line shows a curve predicted by the model; dash lines show standard error intervals for the curve.

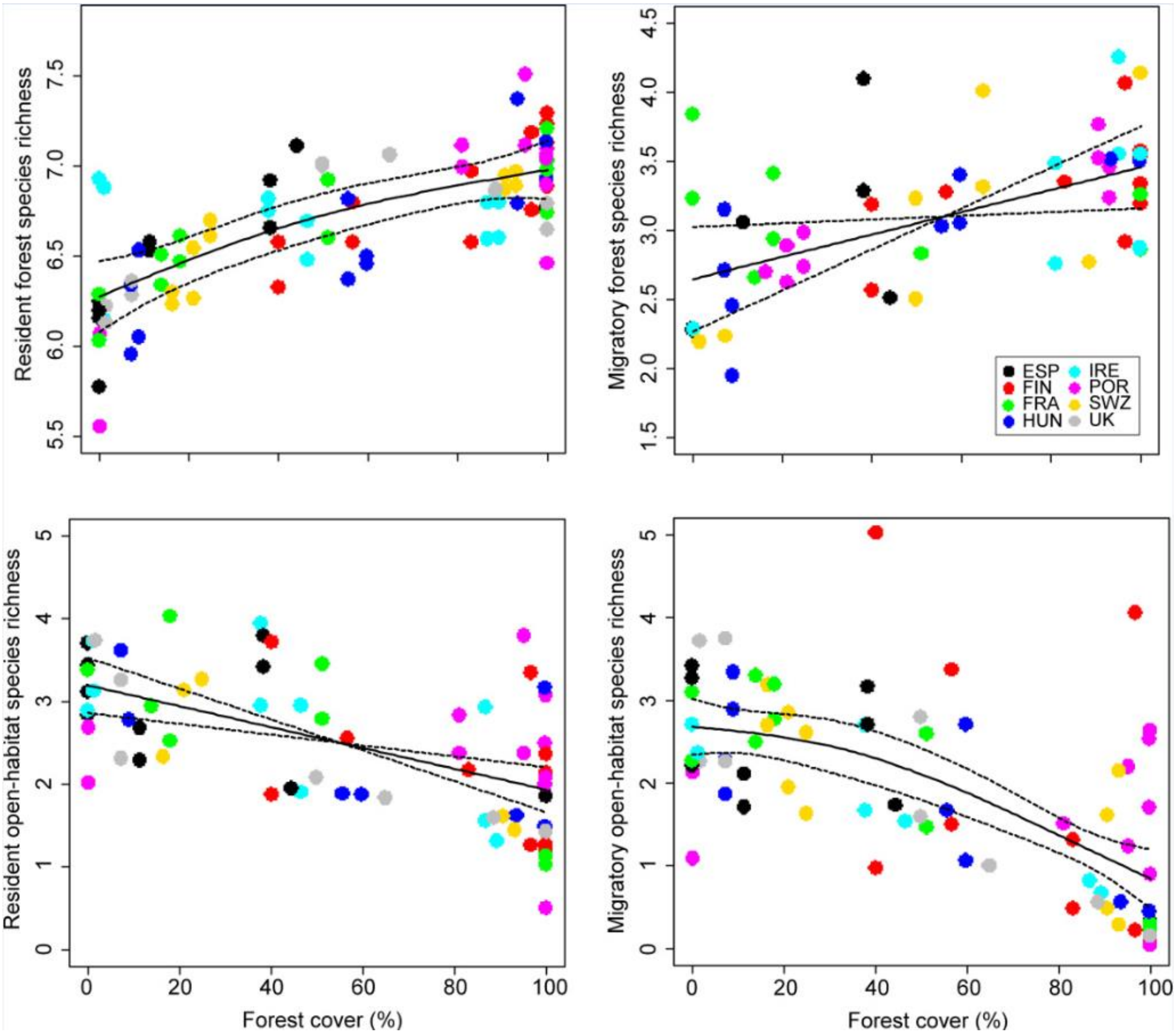

Fig. 3. GAM plots for resident and migratory forest and open-habitat species against forest cover. For other model variables and statistical significance, see Table 2. Residuals for each country are shown with different colors (see legend box); solid line shows a curve predicted by the model; dash lines show standard error intervals for the curve.

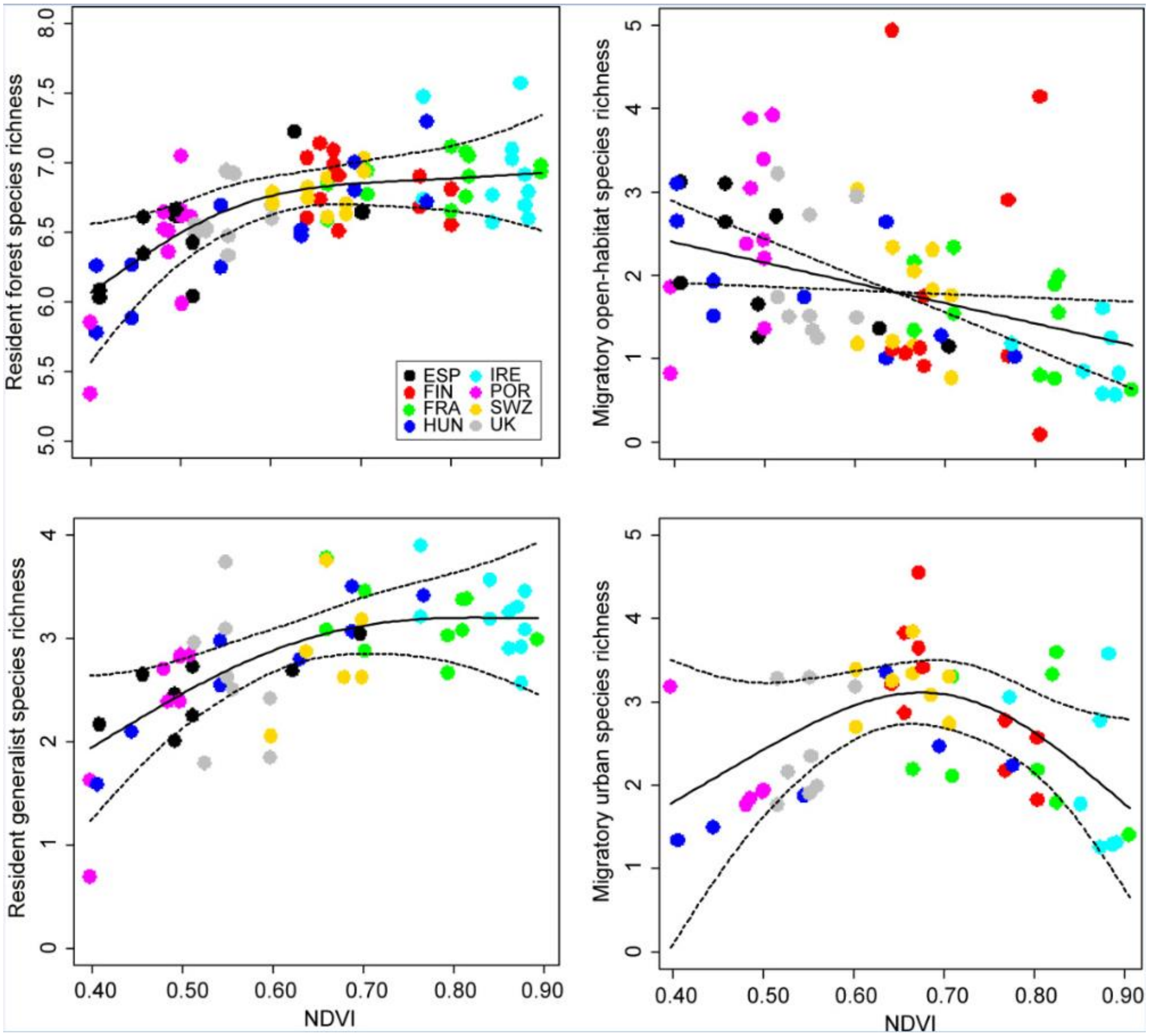

Fig. 4. GAM plots for four groups of species showing significant or marginally significant responses to Normalized Difference Vegetation Index (NDVI). For other model variables and statistical significance, see Table 2. Residuals for each country are shown with different colors (see legend box); solid line shows a curve predicted by the model; dash lines show standard error intervals for the curve.

Table 1. GAM results for different measures of total avian diversity: observed species richness (S_{obs}) and expected richness for 20 and 50 individuals (S_{exp20} and S_{exp50}, respectively). For explanatory variables, see Material and methods; Dev% = percent deviation explained by a given variable; df values for variables subject to smoothing are approximations only (edf); test statistics are either chi-square (for S_{obs} with Poisson distribution) or *F* (for S_{exp} with Gaussian distribution); Curve shape indicates whether a response was increase (Positive) or decrease (Negative), and whether the shape was a straight line (Linear) or not (Concave/Increase+plateau).

Variable	Dev%	edf	Statistic	p	Curve shape
S_{obs} (n = 91; R^2 = 0.71; total deviance = 70.6%)					
Year	0.0	0.0	0.0	0.621	
Country	53.8	6.0	113.6	<0.001	
Forest cover	0.0	1.0	0.1	0.729	
Number of forest patches	1.9	1.0	5.2	0.022	Positive linear
Landscape diversity	3.1	1.0	6.3	0.012	Positive linear
NDVI	1.6	1.8	2.3	0.304	
S_{exp20} (n = 91; R^2 = 0.47; total deviance = 53.2%)					
Year	0.0	0.0	0.0	0.480	
Country	32.9	5.2	6.6	<0.001	
Forest cover	2.4	1.0	3.0	0.089	(Negative linear)
Number of forest patches	1.3	1.0	3.2	0.078	(Positive linear)
Landscape diversity	2.6	1.0	4.2	0.045	Positive linear
NDVI	7.7	2.6	3.1	0.020	Concave/Increase+plateau
S_{exp50} (n = 84; R^2 = 0.55; total deviance = 60.5%)					
Year	0.0	0.0	0.0	0.668	
Country	36.0	5.4	8.0	<0.001	
Forest cover	1.9	1.0	3.0	0.087	(Negative linear)
Number of forest patches	2.0	1.0	4.5	0.037	Positive linear
Landscape diversity	3.5	1.0	6.2	0.015	Positive linear
NDVI	5.3	2.4	2.0	0.082	(Concave/Increase+plateau)

Table 2. GAM results for the species richness of eight ecological groups of birds (for grouping, see Appendix). For explanatory variables, see Material and methods; Dev% = percent deviation explained by a given variable; degrees of freedom are approximations only (edf); test statistics are chi-square; Curve shape indicates whether a response was increase (Positive) or decrease (Negative), and whether the shape was a straight line (Linear) or not (e.g., Increase+plateau or Convex).

Variable	Dev%	edf	Statistic	p	Curve shape
Resident forest species (n = 91; R^2 = 0.86; total deviance = 85.1%)					
Year	1.3	0.6	2.4	0.051	
Country	51.3	6.6	100.6	<0.001	
Forest cover	7.5	1.0	23.3	0.001	Positive non-linear
Number of forest patches	2.6	1.0	8.1	0.005	Positive linear
Forest diversity	0.3	1.0	0.3	0.779	
NDVI	3.3	2.1	4.7	0.091	(Increase+plateau)
Migratory forest species (n = 80; R^2 = 0.93; total deviance = 86.0%)					
Year	0.0	0.0	0.0	0.974	
Country	21.1	5.5	60.6	<0.001	
Forest cover	1.7	1.0	5.8	0.017	Positive linear
Number of forest patches	0.5	1.0	1.4	0.240	
Forest diversity	0.0	1.0	0.2	0.633	
NDVI	0.3	1.3	0.2	0.762	
Resident open-habitat species (n = 91; R^2 = 0.79; total deviance = 73.6%)					
Year	0.0	0.0	0.0	0.451	
Country	28.6	5.4	46.8	<0.001	
Forest cover	6.1	1.0	17.3	<0.001	Negative linear
Number of forest patches	0.4	1.3	0.5	0.764	
Open-habitat diversity	2.6	1.8	6.2	0.060	(Convex)
NDVI	1.4	1.0	3.8	0.052	(Negative linear)
Migratory open-habitat species (n = 91; R^2 = 0.45; total deviance = 54.5%)					
Year	0.0	0.0	0.0	0.549	
Country	10.1	4.3	14.8	0.001	
Forest cover	21.0	1.7	40.5	<0.001	Negative near-linear
Number of forest patches	0.6	1.5	1.0	0.421	
Open-habitat diversity	1.3	1.0	2.5	0.115	
NDVI	2.4	1.0	6.0	0.014	Negative linear
Resident generalists (n = 79; R^2 = 0.76; total deviance = 69.4%)					
Year	0.0	0.0	0.0	0.872	
Country	40.4	5.1	32.4	<0.001	
Forest cover	1.0	1.0	1.0	0.310	
Number of forest patches	1.1	1.5	1.2	0.268	
Landscape diversity	0.3	1.0	0.1	0.741	
NDVI	7.6	1.9	6.5	0.043	Increase+plateau
Migratory generalists (n = 74; R^2 = 0.71; total deviance = 65.7%)					

Year	0.0	0.0	0.0	0.375	
Country	28.8	5.4	30.2	<0.001	
Forest cover	0.6	1.0	1.3	0.245	
Number of forest patches	1.1	1.0	2.2	0.135	
Landscape diversity	0.7	1.0	1.2	0.280	
NDVI	0.4	1.0	0.5	0.502	
Resident urban species (n = 91; R^2 = 0.77; total deviance = 75.5%)					
Year	0.0	0.0	0.0	0.812	
Country	54.2	6.6	90.0	<0.001	
Forest cover	0.1	1.0	0.1	0.775	
Number of forest patches	1.2	1.0	2.2	0.143	
Landscape diversity	0.8	1.0	0.9	0.333	
NDVI	3.4	1.8	4.1	0.125	
Migratory urban species (n = 68; R^2 = 0.85; total deviance = 75.0%)					
Year	0.0	0.0	0.0	0.773	
Country	20.1	3.3	20.1	<0.001	
Forest cover	3.0	1.0	2.9	0.109	
Number of forest patches	-0.1	1.0	0.0	0.911	
Landscape diversity	2.1	1.0	3.2	0.075	(Positive linear)
NDVI	4.1	1.8	6.1	0.054	(Concave)

Table S1. Percent covers of forest and agricultural land variables for each land-use unit (LUU) derived from remote-sensed data. Arable = arable land; Pasture = open pastures and pastures with scattered trees; Grassland = meadows; Other agr. = other types of agricultural land; Forest = forest land (with different successional stages); Scrub = scrub land; Wetland = bogs, ponds, etc.; Other = other habitat types (artificial surfaces, open water, etc.). Row sums may not make up exactly 100 because of rounding to the nearest integer.

Country	LUU	Arable	Pasture	Grassland	Other agr.	Forest	Scrub	Wetland	Other
Spain (ESP)	1	6	-	-	-	44	35	-	15
	2	-	-	-	-	99	1	-	-
	3	23	-	19	-	-	58	-	-
	4	-	-	37	11	38	6	-	8
	5	-	-	83	6	11	-	-	-
	6	59	-	25	-	-	16	-	-
Finland (FIN)	1	-	-	-	-	100	-	-	-
	2	-	-	-	-	100	-	-	-
	3	3	-	1	-	97	-	-	-
	4	7	-	2	8	83	-	-	-
	5	25	-	10	9	57	-	-	-
	6	57	-	3	-	40	-	-	-
France (FRA)	1	-	-	-	-	100	-	-	-
	2	-	-	-	-	100	-	-	-
	3	3	45	-	-	51	-	-	-
	4	5	81	-	-	14	-	-	-
	5	-	82	-	-	18	-	-	-
	6	16	84	-	-	-	-	-	-
Hungary (HUN)	1	-	-	-	-	100	-	-	-
	2	-	-	2	-	94	-	-	4
	3	27	-	13	-	60	-	-	-
	4	32	-	13	-	56	-	-	-
	5	-	-	91	-	9	-	-	-
	6	77	-	7	-	7	-	-	9
Ireland (IRE)	1	3	-	9	-	87	-	-	1
	2	-	-	11	-	89	-	-	-
	3	3	-	51	-	46	-	-	-
	4	46	-	13	-	38	-	-	3
	5	-	-	99	-	-	-	-	1
	6	86	-	12	-	1	-	-	1
Portugal (POR)	1	-	-	-	16	81	-	-	2

	2	-	-	-	-	100	-	-	-
	3	-	4	-	-	95	1	-	-
	4	-	-	-	-	100	-	-	-
	5	-	-	-	-	100	-	-	-
	6	-	19	-	81	-	-	-	-
Switzerland (SWZ)	1	-	-	6	-	91	-	-	4
	2	-	-	7	-	93	-	-	-
	3	-	-	46	-	54	-	-	-
	4	-	-	72	-	25	-	3	-
	5	-	-	75	-	16	-	-	9
	6	-	-	68	-	21	-	-	10
United Kingdom (UK)	1	-	-	-	-	100	-	-	-
	2	-	-	-	-	89	-	-	11
	3	-	-	17	-	65	18	-	-
	4	17	-	31	2	50	-	-	-
	5	35	-	58	-	7	-	-	-
	6	50	-	42	-	2	2	-	3

Spatial autocorrelation

We assessed the extent of spatial autocorrelation by calculating Moran's *I* based on residuals from the GAMs for each dependent variable using the Moran.I command in the package Ape (Paradis et al. 2017). Although country was included as a random variable in the models in order to account for larger scale spatial effects, the Moran's test suggested there was significant negative autocorrelation for the three estimates of species richness for the whole community, i.e. S_{obs}, S_{exp20} and S_{exp50} (Table S2). This suggests that sites closer together were less similar than those further apart. Negative autocorrelation values appear a norm in GAMs but strongly negative values may indicate over-fitting (Wood 2017). We attempted to overcome this issue by setting the maximum df = 2 and by using a smoothed interaction latitude × longitude instead of country, but the significant negative autocorrelation persisted. However, the results remained similar, with only marginal changes in test statistics, *p* and approximations of df, so the presented models were probably robust (unpubl. data). Nevertheless, we further explored the spatial distribution of residuals using bubble plots (as per Zuur et al. 2009). Fig. S1 shows that there was little evidence of obvious clustering of sites with particularly positive or negative residuals. However, it was clear that the Portuguese site (the most southerly in Fig. S1) had strongly negative residuals. When models were re-run without Portugal, there was no evidence of spatial autocorrelation (S_{obs} $I = -0.06$, $p = 0.376$; S_{exp20} $I = -0.06$, $p = 0.412$; S_{exp50} $I = -0.08$, $p = 0.282$). When dropping other countries in turn, the significant spatial autocorrelation remained, thus supporting the notion that the results in Table S2 were driven by data from a single country. GAMs were re-run without Portugal for S_{obs}, S_{exp20} and S_{exp50}. Results were broadly similar (Table S3), in that the form of the relationship (i.e., edf) and significance were similar (at least significant results in one data set was accompanied by a result that approached significance in the other, i.e., $p < 0.09$), although there was no longer a significant effect of forest fragmentation on species richness.

There was no evidence of spatial autocorrelation in the group-specific measure of species richness, with the exception of resident generalists where there was a weak negative autocorrelation (Table S2). For this group, by setting the maximum df = 2 and replacing Country with the smoothed interaction latitude × longitude accounted for the autocorrelation somewhat better ($I = -0.10$, $p = 0.079$), but the GAM results remained similar. Thus, generally, Country apparently accounted for spatial autocorrelation rather well.

In summary, the significant negative spatial autocorrelations observed appear to have been due to outlier effects, rather than genuine ecological effects across the whole sample. Omitting Portuguese data did not result in major differences in the effects of explanatory variables measuring the whole community. For resident generalists, incorporating continuous smoothed spatial coordinates reduced the extent of spatial autocorrelation, but there was little effect on the GAM results. We therefore conclude that, whilst there was statistically significant spatial autocorrelation, this was not ecologically significant and did not affect the interpretation of model outputs on bird community measures.

References

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Wood, S.N. 2017. *Generalized additive models. An introduction with R. Second edition*. – CRC Press, Taylor & Francis Group, Boca Raton.

Zuur, A. et al. 2009. *Mixed effects models and extensions in ecology with R*. – Springer, New York, NY, USA.

Table S2. GAM models (compare Tables 1−2) with associated Moran's test statistics (observed value, expected value with standard deviation, and probability for accepting the null hypothesis of no autocorrelation).

Model	**Obs.**	**Exp.**	**SD**	**p**
S_{obs}	-0.17	-0.01	0.04	<0.001
S_{exp20}	-0.18	-0.01	0.05	<0.001
S_{exp50}	-0.19	-0.01	0.05	<0.001
Resident forest species	-0.09	-0.01	0.05	0.114
Migratory forest species	-0.01	-0.01	0.05	0.930
Resident open-habitat species	-0.07	-0.01	0.05	0.266
Migratory open-habitat species	-0.05	-0.01	0.05	0.480
Resident generalists	-0.12	-0.01	0.05	0.031
Migratory generalists	0.04	-0.01	0.06	0.334
Resident urban species	-0.07	-0.01	0.05	0.223
Migratory urban species	0.04	-0.01	0.06	0.383

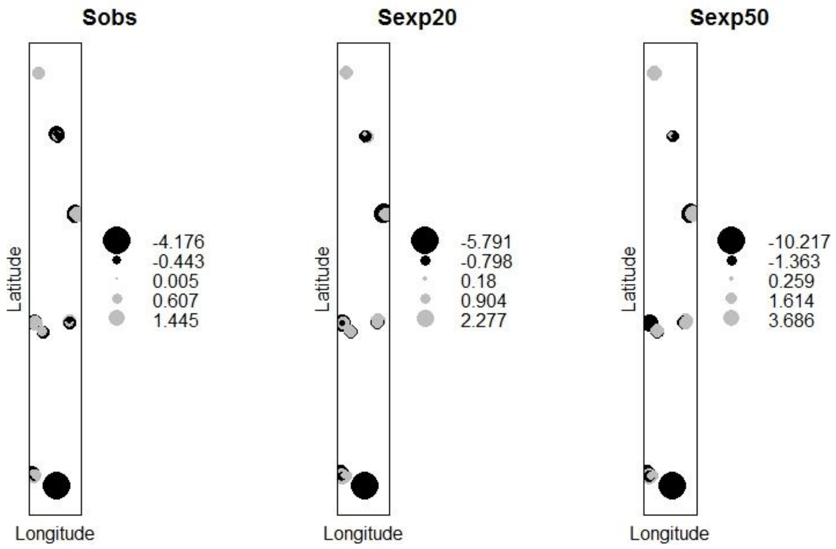

Fig. S1. Bubble plots of residuals plotted against geographic location. The order of the countries from north to south is: Finland, UK, Ireland, France, Hungary, Switzerland, Spain and Portugal.

Table S3. Model outputs for the whole sample (i.e., eight countries) and for a reduced data set without Portugal for the three dependent variables that showed evidence of relatively strong spatial autocorrelation; S_{obs}, S_{exp20} and S_{exp50}. edf indicates the estimated degrees of freedom, where 1 indicates a linear relationship, and higher values indicate increasingly non-linear associations. Statistic indicates χ^2 for S_{obs} (i.e., model specifying normal errors) and an *F* test for S_{exp20} and S_{exp50} (Gaussian errors).

		Whole sample			Without Portugal		
Dependent	Predictor	edf	Statistic	*p*	edf	Statistic	*p*
S_{obs}	Year	0.00	0.00	0.621	0.00	0.00	0.301
	Country	6.04	113.57	<0.001	5.25	104.94	<0.001
	Forest cover	1.00	0.12	0.729	1.00	1.471	0.225
	No. forest patches	1.00	5.43	0.022	1.00	2.38	0.123
	Landscape diversity	1.00	6.32	0.012	1.00	6.19	0.013
	NDVI	1.75	2.32	0.331	1.00	0.49	0.483
S_{exp20}	Year	0.00	0.00	0.480	0.00	0.01	0.023
	Country	5.18	6.60	<0.001	4.46	9.73	<0.001
	Forest cover	1.00	2.96	0.089	1.99	12.96	<0.001
	No. forest patches	1.00	3.20	0.078	1.09	2.87	0.087
	Landscape diversity	1.00	4.17	0.045	2.56	8.51	<0.001
	NDVI	2.57	3.15	0.032	1.88	8.15	<0.001
S_{exp50}	Year	0.00	0.00	0.668	0.00	0.00	0.085
	Country	5.42	8.03	<0.001	4.69	12.54	<0.001
	Forest cover	1.00	3.00	0.087	1.97	15.30	<0.001
	No. forest patches	1.00	4.53	0.037	1.00	3.62	0.062
	Landscape diversity	1.00	6.18	0.015	2.62	8.88	<0.001
	NDVI	2.37	1.95	0.133	1.68	2.52	0.089

Table S4. Spearman correlation coefficients (rho) and associated probabilities between growing degree days (source: https://www.atlas.impact2c.eu/en/climate/growing-season-length/) and 11 bird species groups (averages; n = 8).

Species group	**rho**	***p***
S_{obs}	0.18	0.670
S_{exp20}	-0.16	0.713
S_{exp50}	-0.23	0.588
Resident forest species	0.63	0.092
Migratory forest species	-0.77	0.024
Resident open-habitat species	0.89	0.003
Migratory open-habitat species	-0.80	0.016
Resident generalists	0.47	0.244
Migratory generalists	-0.61	0.111
Resident urban species	0.54	0.171
Migratory urban species	-0.85	0.008

Table S5. GAM for avian diversity measures and four specialist groups with only Year, Country and Forest cover as explanatory variables. Gaussian error distribution with associated chi-square statistics was applied for S_{exp20} and S_{exp50}; Poisson error distribution and F statistics for the rest. For more details concerning variables, see text.

Variable	edf	Statistic	p
S_{obs} (Full model deviance = 67.5%; R^2 = 0.68; n = 91)			
Year	0.0	0.0	0.636
Country	6.5	137.4	<0.001
Forest cover	2.1	10.2	0.007
S_{exp20} (Full model deviance = 40.9%; R^2 = 0.36; n = 91)			
Year	0.0	0.0	0.499
Country	5.6	6.0	<0.001
Forest cover	1.9	2.9	0.046
S_{exp50} (Full model deviance = 52.8%; R^2 = 0.48; n = 84)			
Year	0.0	0.0	0.655
Country	6.0	8.9	<0.001
Forest cover	2.0	5.9	0.004
Resident forest species (Full model deviance = 79.6%; R^2 = 0.82; n = 91)			
Year	0.7	2.8	0.044
Country	6.7	139.3	<0.001
Forest cover	2.5	31.1	<0.001
Migratory forest species (Full model deviance = 85.5%; R^2 = 0.93; n = 80)			
Year	0.0	0.0	0.974
Country	5.5	160.7	<0.001
Forest cover	1.5	5.4	0.039
Resident open-habitat species (Full model deviance = 69.7%; R^2 = 0.67; n = 91)			
Year	0.0	0	0.432
Country	6.3	92.28	<0.001
Forest cover	1.0	32.35	<0.001
Migratory open-habitat species (Full model deviance = 53%; R^2 = 0.47; n = 91)			
Year	0.0	0.0	0.518
Country	6.1	22.4	0.001
Forest cover	2.2	60.4	<0.001

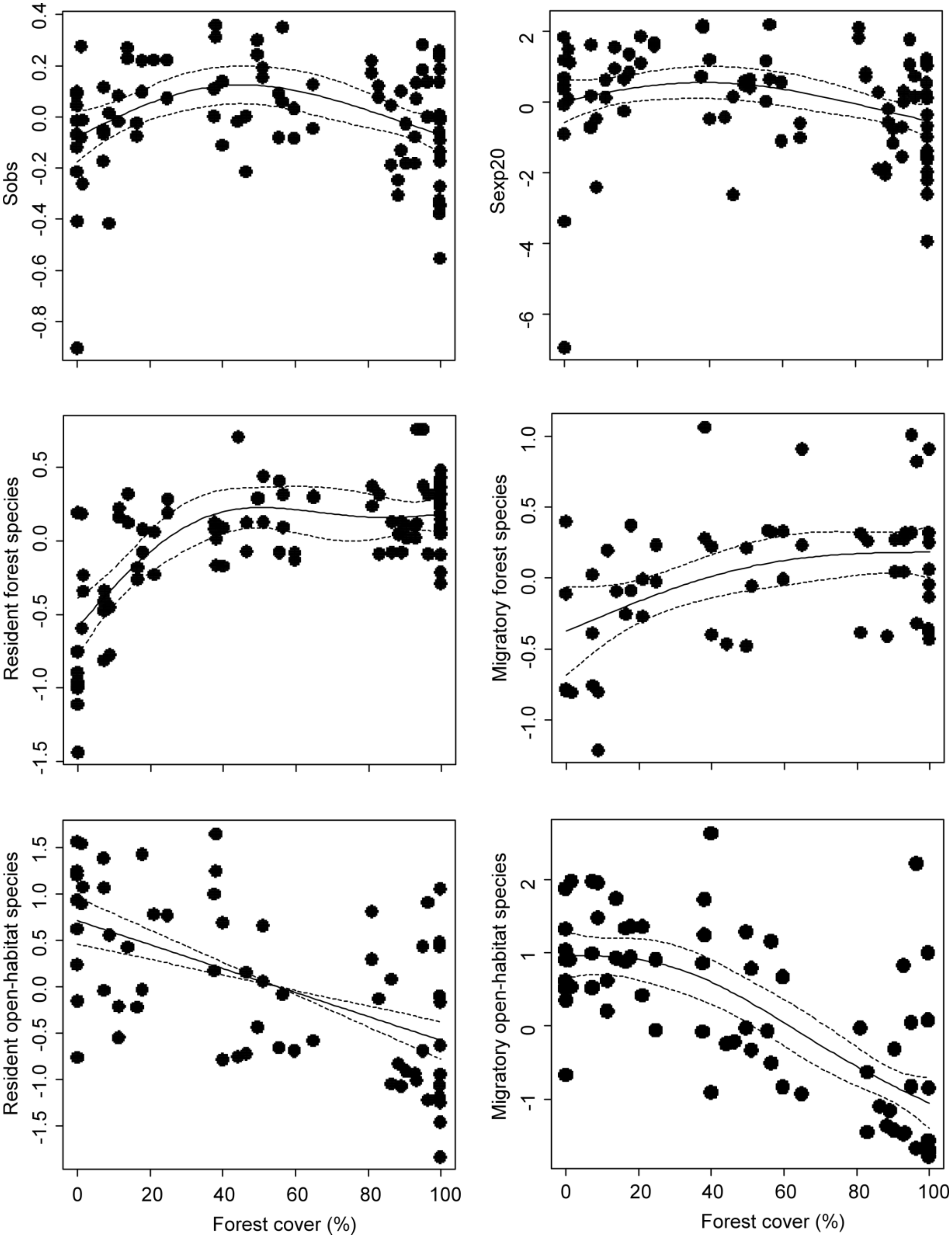

Fig. S2. GAM plots associated with Table S5. The curves (average and SE) are centered to Y-axis zero by the plotting default of mgcv (Wood 2017). Black dots are residuals for different combinations of year, country and LUU (see text).