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# Bird communities of a temperate forest: spatio-temporal partitioning between resident and migratory species

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## ABSTRACT

A lot of bird species are declining in Europe and studies of bird community assembly are fundamental to propose efficient conservation actions. Many studies were carried out on the regional variability of abundance and distribution of bird communities, but few studies considered the local patch variability. In this study, we worked on intra-patch variability of breeding bird community in the forest patch of Corbière (Britanny, France). We tested whether bird community distribution was related to habitat characteristics and whether distribution patterns depended on life history traits of species. During three years, we used a regular sampling and the point count method to sample whole bird community within this forest patch. Our results showed that several biotic and abiotic variables - distance to forest edge, deciduous tree cover, coppice cover, elevation - controlled individual abundances of bird species as well as indicators of bird community - abundance, diversity, evenness. Moreover, we found that abundances of resident birds, short-distance migrants and long-distance migrants were differently related to biotic and abiotic variables, and that these relationships varied within the breeding season. We suggest that this space partitioning may be explained by the temporal dynamics of the bird community: resident and short-distance species were present earlier than long-distance species in the forest patch, and might preferentially choose high quality habitats. Long-distance migrants arrived later in the breeding season and might not find the same habitat availability, they might consequently only nest close to the forest edge, in high sites or sites with sparse understory. Our results show that local studies, taking into account migratory status and species dynamics at intra-season scale, are important keys to understand distribution patterns which are observed along entire breeding seasons.

**Keywords:** forest biodiversity, bird community, species partitioning, migratory status, temporal dynamics

# INTRODUCTION

The study of bird communities is often used to determine indicators of health of natural habitats under global changes (Canterbury *et al*. 2000, Gregory *et al.* 2007). Specifically, studies of bird communities permit identification of population trends: for instance, Gregory *et al*. (2007) found a sharp decline (-13 % over the period 1990-2002) of forest birds in Western Europe. Population trends may depend on life history traits of species: Julliard *et al*. (2003) and Jiguet *et al*. (2007) showed, noteworthy, the decline of specialist species – in France, this decline is moderate in protected areas but is accentuated in areas without special status (Devictor *et al*. 2007). Moreover, it has been shown that among European forest birds, long-distance migrants declined more strongly than short-distance migrants or permanent residents (Sanderson *et al*. 2006, Gregory *et al*. 2007). Arrival dates of migratory birds became earlier in recent decades, in particular for early migratory species (Tryjanowski *et al*. 2005), as did the starting dates for fall migration of long-distance migrants (Jenni & Kéry 2003) and broods production (Both & Visser 2001). Overall, global changes have strong effects on bird communities, and these effects depend on ecology and life history traits of bird species, especially their breeding phenology. As efficient practices of protection and conservation became crucial for maintaining avian biodiversity, we need to understand the mechanisms driving local bird abundance and distribution (Raymond *et al.* 2010, Balestrieri *et al.* 2015). According to studies at regional scales, forest bird communities can be driven by deterministic or random processes (Renner *et al.* 2014) and many studies were already conducted at this scale to identify deterministic processes, *i.e.* biotic and abiotic factors governing distribution of forest bird communities, such as forest composition and structure, and amount and nature of forest edges (Martin-Morales 2005, Goetz *et al.* 2010).

First, tree species composition and structure of forest patch drive bird community distribution. The density and age of trees can determine community species richness (James & Warner

1982, Berg 1997, Poulsen 2002). Spatial heterogeneity of tree species distribution may increase overall bird abundance and increase abundance of specific functional groups (Freemark & Merriam 1986). Moreover, the composition of forest stands - deciduous *vs* coniferous dominance - is a very important factor in habitat selection by species, since many species have distinct habitat and resource preferences (James & Wamer 1982, Patterson & Best 1996, Berg 1997). More recent studies also showed that heterogeneity of vertical structure and height of canopy can increase the richness of migratory birds (Goetz *et al*. 2007, 2010). Finally, available resources, often related to moisture in forest habitats due to tree density (Petit *et al*. 1985), and forest productivity may increase bird species richness (Cody 1981, Böhm & Kalko 2009).

Second, the amount and nature of forest edges drive bird community distribution. It has been shown that the amount of edges, subject to higher predation and parasitism, could reduce overall avian biodiversity in forest patches and strongly decrease abundance of specific functional groups preferring forest core (Herkert 1994, Deng & Gao 2005, Ludwig *et al.* 2012). There may, however, exist some species preferring the edge, mainly depending on their diet (Kroodsma 1984, McCollin 1998, Martinez-Morales 2005). Overall, the role of edges has been importantly debated in ecology and if their negative impact of avian biodiversity has been recognized, a consensus assessed that edge effects strongly depend on the matrix surrounding the forest patch (Donovan *et al.* 1997). Noteworthy, the contrast between forest resources and landscape resources (Ries & Sisk 2004) and the specific interactions between forest species and openfield species (Fagan *et al.* 1999) are important drivers of edge effect on bird communities.

We observe very different responses of bird communities to the previously-listed habitat factors according to life history traits of bird communities (Lynch & Whigham 1984, Estades & Temple 1999, Hansbauer *et al*. 2010, Gharehaghaji *et al*. 2012). Life history traits illustrate ecological strategy of species to respond to biotic and abiotic conditions, and permit a mechanistic understanding of the relationships between environmental factors and species distribution (Caprio *et al.* 2008). Clearly, the migratory status - resident, short and long-distance migrant - is an important trait of bird species, which can explain spatial distribution patterns of bird communities (Lynch & Whigham 1984, Flather & Sauer 1996, Korňan *et al.* 2013). Resident and migratory species have indeed different periods of presence in forest patches and thus different temporal dynamics, which lead to different spatial distributions and to seasonal variation in spatial distributions (Griffis-Kyle & Beier 2005, Böhm & Kalko 2009).

Most studies on breeding bird distribution in wooded areas focused on landscape or regional scale. At these scales, inter-patch comparisons (size, shape, composition) were designed to explain the variability of bird communities between patches. However, efficient conservation practices often occur at local scale, which is the scale on which management projects are the more easily carried out. Studies looking for mechanisms driving bird distribution at intra-patch scale are scanty (Proença *et al.* 2010, Albanese & Davis 2015, Isotti *et al.* 2015). Furthermore, few studies considered the temporal dynamics depending on the migratory status of species, despite this status was often studied at larger scales. In this study, we proposed to analyse within a same forest patch the relationships between bird species distribution and environmental variables (habitat characteristics) in connection with bird migratory status and intra-season dynamics. Based on previously published work, we addressed the following questions: (i) Do environmental variables explain the distribution of bird species? (ii) Do the distribution patterns depend on the migratory status of species? (iii) Do the distribution patterns vary within the breeding season? We used the point count method to sample the whole bird community of the forest patch of Corbière (Britanny, France), during three years, and using a regular seasonal sampling procedure. We collected a full set of relevant environmental variables and tested relationships between bird community and environmental variables, at different times of the breeding season and depending on the migratory status of species.

## MATERIALS AND METHODS

### *Study area*

The study was carried out in the forest patch of Corbière, located 15 kilometers east of the city of Rennes, Brittany, France (48° 14'N, -1° 39'W) and extending 740 hectares (Figure 1). The study area is the property of "Conseil Départemental d'Ille-et-Vilaine" who issued permission for field surveys. This study involved protected species (passerine community) but was only based on audiovisual observations and did not require any official authorization nor ethic committee statements. The forest patch is surrounded by a typical Breton agricultural landscape, which has undergone significant land reparcelling but retains a high degree of heterogeneity. It is a mixed temperate forest mainly composed of deciduous trees belonging principally to *Quercus petraea* and *Quercus pedunculata* series. There is a wide range of ecological conditions, especially related to local topography, forest stands and local management – management depends on the owners of the forest stands and is, overall, few intensive.

### *Composition and abundance of bird community*

The study focused on the forest breeding bird community during the nesting period extending from April to June. The sampling period was in accordance with recommandations of Ralph *et al.* (1995). It involved all potentially breeding bird species in the forest patch so it was mainly based on the community of passerines (see Appendix 1) with mainly understory nesters. Data were collected by the method of point counts (e.g. Holmes *et al.* 1986). A grid with a mesh size of 500 m was positioned on the forest, and 29 bird point counts were regularly distributed on the mesh grid to cover the entire forest patch (Figure 1). As one year of study appears insufficient to validate habitat/species relationships (Adamik & Kornan 2004), we performed the study over 3 years, from 2008 to 2010, with three field sessions at each spring (once per month: April, May, June) to accurately describe the breeding bird community at each point count. During the three annual field sessions, the 29 point counts were sampled within 3 hours from sunrise with a period of listening and observation of 15 minutes at each point, in standardized surveys conditions. All encountered species were recorded, by taking into account only encounters with different individuals, according to the following nomenclature: 1 for songbirds, couples, occupied nests and family groups, and 0.5 for solitary birds seen or heard (songs or calls), to take into account that some birds may be migrating or passing by and did not belong to the local community. We assigned the migratory status of bird species - residents, short-distance migrants and long-distance migrants - using the atlas of Dubois *et al.* (2008) and "Groupe ornithologique Breton" (2012).

*Composition and structure of forest patch*

The Office National des Forêts (ONF) conducted a complete mapping of the forest in the massif of Corbière in 2007, concerning forest stands and habitats: tree species composition, coppice cover, number of dead trees and cavities as well as information on the forest structure with the basal area (reflecting the density and age of the grove, *i.e.* the sum of the surfaces of each section of tree at 1.30 meter above the ground, in m²/ha). The distribution of stands dominated by deciduous or coniferous trees within the forest patch is shown on Figure 1. A Digital Terrain Model (DTM) was performed to describe patch topography, giving us a quantitative elevation variable at each point count (Figure 1). All information were compiled with a GIS (Geographic Information System, ArcGIS 10 software). Then, we used a buffer of 200 m radius to quantify the previously-listed environnemental variables around the point counts. We also calculated a distance to the forest edge for each point count. Finally, we calculated an heterogeneity index of the tree composition around the point counts; this index was based on the cumulative stand area distribution and was interpreted as the probability that two randomly chosen pixels in the patch were not situated in the same stand (DIVISION index, software Fragstats 4.1., McGarigal *et al.* 2012). All variables used in analyses are shown in Appendix 2.

*Data analysis*

Prior to analyses we center-reduced all data, *i.e.* transformed variables by subtracting their mean and dividing by their standard deviation, as it ensures regression coefficients are comparable among models. First, we performed a co-inertia analysis (Chessel *et al*. 2003) to evaluate relationships between distribution of individual bird species and environmental variables. To conduct this analysis, we used a matrix of cumulative maximal abundances, *i.e.* containing for each point count the sum of the maximal abundances observed for each species during the three years; maximal abundances at each year were obtained using the highest abundance observed along the three annual surveys (April, May, June). Only 35 out of the 54 bird species recorded were considered for this co-inertia analysis, to exclude very rare species that would affect the analysis disproportionally to their abundance (the criteria was species present in less than 3 among the 29 point counts). To perform the co-inertia analysis, a factorial correspondance analysis (COA) was first performed on the matrix of cumulative maximal abundances, then, a principal component analysis (PCA) weighted by the lines of the COA (Chessel *et al*. 2003) was carried out on the matrix of environmental variables– excluding redundant environmental variables after prior selection on the matrix of correlations. The co-inertia analysis was finally performed to evaluate covariation between COA and PCA.

Then, we used mixed models (see Zuur *et al.* 2009) to explain bird community indicators (total abundance, diversity, evenness, abundance of residents, short-distance migrants and long-distance migrants) by environmental variables and month of the breeding season. We used for each month the sum of abundances observed during the three years. Environmental variables were the fixed effects, and month was the random effect – i.e. a 3-level random effect, which is relevant for a random effect (Gelman & Hill 2007). For each dependent variable, we constructed an initial model containing all the fixed effects and the random effect (fixed effects: distance to edge, coniferous tree cover, deciduous tree cover, coppice cover, elevation, heterogeneity, basal area; random effect: month), and we optimized the model using a backward stepwise selection procedure of explanatory variables, keeping the significant variables only. Random effects were significant when their range of values, i.e. lower/estimate/upper, excluded the zero value. We used the “nlme” package under R software. The best model was selected based on AIC and BIC (Burnham & Anderson 2002; Chen & Chen 2008). We tested spatial dependancy of residuals using Moran's I, and all results, despite a slight trend of overdispersion, were non-significant.

Finally, we used multiple ordinary least square regression models to test the relationship between environmental variables and abundances of residents, short-distance migrants and long-distance migrants, at each month of the breeding season. For each dependent variable, we constructed an initial model containing all independent variables, and we optimized the model using a backward stepwise selection procedure of explanatory variables. We tested spatial dependancy of residuals using Moran's I, and all results were clearly non-significant. Here and in previous analyses, distribution of bird community indicators fulfilled normality and homogeneity, we also graphically explored residuals using probability plots and predicted *vs* residual plots and residuals fulfilled normality and homogeneity. All statistical analyses were performed with R 3.3.1 software (R Development Core Team, 2016).

## RESULTS

### *Relationship between individual abundance of bird species and environmental variables*

Co-inertia analysis (Figure 2) was highly significant (*P*=0.001), with a correlation coefficient RV=0.50, and the two first axes supported 62% of the total variance of the original two matrices. This indicates that several variables explained bird species distribution. These variables were the deciduous or coniferous tree cover (first axis), elevation (first axis), distance to forest edge, basal area, coppice cover and heterogeneity of tree composition (second axis). For instance, we observed that basal area increased abundance of the Eurasian Sparrowhawk (*Acni*). Meanwhile, the distribution of the Middle Spotted Woodpecker (*Deme*) was influenced by deciduous trees, like the Short-toed Treecreeper (*Cebr*) and the Eurasian jay (*Gagl*). We also observed that when distance to forest edge increased, abundance of migratory species like the Eurasian Golden Oriole (*Oror*) and the Garden Warbler (*Sybo*) declined. The Tree Pipit (*Antr*) and the Common Chiffchaff (*Phco*) principally followed coniferous tree cover, whereas the Common Firecrest (*Reig*) responded strongly to the coppice cover and the heterogeneity of tree composition.

### *Effect of environmental variables on bird community structure*

Various environmental variables significantly explained bird community indicators, and strongly explained abundance of residents, short-distance migrants and long-distance migrants ($R^2$ ranging from 0.26 to 0.45, Table 1). The month of sampling - random effect - significantly influenced total abundance of bird community as well as abundance of residents and long-distance migrants. This indicates, across the entire forest patch, intra-month and inter-month differences in total abundance of bird community and abundance of residents and long-distance migrants. Distance to edge decreased total abundance and diversity of bird community, as well as abundance of short-distance migrants. Deciduous tree cover increased total abundance and diversity of bird community. Elevation decreased evenness of bird community, and was also the variable that discriminated the most bird abundances depending on migratory status: elevation decreased abundance of residents, while it did not change abundance of short-distance migrants, and increased abundance of long-distance migrants (Fig. 3). Also, basal area decreased abundance of short-distance migrants. Finally, coppice cover decreased abundance and diversity of bird community, and decreased abundance of short-distance migrants. Overall, we observed that abundances of residents, short-distance migrants and long-distance migrants were differently related to environmental variables.

*Distribution patterns of residents, short and long-distance migrants along the breeding season*

Within the three months of the breeding season, environmental variables well explained abundances of residents, short-distance migrants and long-distance migrants ($R^2$ ranging from 0.10 to 0.38, Table 2). The distribution pattern of short-distance migrants was quite the same along the breeding season: for all months of the season, abundance of short-distance migrants decreased with distance to edge and coppice cover (Table 2, Figure 4). Meanwhile, abundance of residents and long-distance migrants showed different distribution patterns along the breeding season (Table 2, Figure 4). From graphical illustrations in Figure 3, we learned more from the random effect of the month we observed in the mixed models, since we observed that abundances of residents were higher at the two first months of the breeding season (April and May), while abundances of long-distance migrants were higher at the two last months of the breeding season (May and June). Abundances of short-distance migrants remained quite the same along the entire breeding season, consistently with the non-significance of the random effect of the month in the mixed model (see Tab. 1). Overall, we observed that three of the six variables influencing abundance of both residents and short-distance migrants within the breeding season, acted with the same sign on these abundances (distance to edge, deciduous tree cover, coppice cover). Consequently, at the middle of the breeding season (May), residents and short-distance migrants displayed very similar responses to environmental variables. On the other hand, three of the six variables influencing long-distance migrants within the breeding season acted with an opposite sign on abundance of residents or short-distance migrants (distance to edge, elevation, heterogeneity)

## DISCUSSION

### *Environmental variables drove bird species distribution*

We showed that bird species distribution strongly depended on environmental variables, which were coniferous or deciduous tree cover, distance to forest edge, elevation and basal area. Our results show that at intra-patch scale, distribution patterns can be deterministic and not stochastic, like observed in some studies (Renner *et al.* 2014). Some species had a clear preference for high zones (European Turtle Dove) or low zones (Middle-Spotted Woodpecker), coniferous zones (Tree Pipit, Crested Tit) or deciduous zones (Shy Jay, Short-toed Treecreeper), forest edges (Eurasian Golden Oriole, Garden Warbler) or forest core (Great-Spotted Woodpecker, Goldcrest). In contrast, other generalist species such as the Common Chaffinch or European Robin were present and equally abundant in all point counts. Overall, these relationships probably resulted from habitat selection of bird species, which depended on the precise ecological traits of each species (foraging, use of strata, nesting, migration). Our results are hence consistent with studies showing, for instance, an effect of edge (Kroodsma 1984, Ludwig *et al.* 2012) or composition of the forest stand (Patterson & Best 1996, Castaño-Villa 2014) on individual bird species distribution. Finally, we observed that variables driving distribution patterns at intra-patch scale may be similar to variables acting at regional scale (Korňan *et al.* 2013) but may act in very different ways on bird species distribution.

### *Environmental variables explained bird community structure*

We also observed that indicators of bird community structure were related to environmental variables. Specifically, we showed that elevation decreased evenness of bird community, indicating high zones harbored more rare species. A consistent result was found in a forest mosaic in northern Europe by Luoto *et al.* (2004), where bird species richness was greater in forests with steep topography. This result is also consistent with general theories in ecology assessing that a tridimensional habitat improves biodiversity, by improving the number of available niches, and consistent with studies on altudinal gradient assessing an increase of species richness with slight elevation (Loiselle & Blake 1991, Grytnes & Vetaas 2002). Moreover, deciduous tree cover increased abundance and diversity of bird community. We might propose that deciduous zones provided a range of habitats and resources which was larger than that of coniferous zones. Also, coppice cover decreased abundance and diversity of bird community, suggesting birds preferred clear zones with sparse understory to nest. Finally, distance to edge decreased abundance and diversity of bird community. This last result indicates that bird community benefited from the proximity of forest edge, and hence indicates a positive edge effect. This result challenges the frequent observations of negative edge effects at the landscape scale (Rodewald 2002, Batary & Baldi 2004, Deng & Gao 2005, Ludwig *et al.* 2012). From other studies (Penhollow & Stauffer 2000, Bulluck & Rowe 2006, Vetter *et al.* 2013), we might suggest that the forest edge, surrounded by an agricultural landscape which conserves a high degree of heterogeneity, was a zone of high ecological diversity and biotic interactions rather than a zone of high perturbation.

### *Spatial partitioning between resident and migratory birds*

Our results clearly showed a spatial partitioning between resident and migratory birds. Short-distance migrants were located mainly close to the forest edge, in sites with sparse understory and low tree density. Residents preferred low sites, whereas long-distance migrants preferred high sites. Local environmental factors play therefore an important role for habitat selection in bird species depending on the migratory status of species. These results are new because no study, to our knowledge, showed an influence of phenology on habitat selection at intra-patch scale. The positive edge effect observed on abundance of short-distance migrants contradicts previous studies at the regional scale which found that fragmentation, resulting in increased forest edges, decreased migratory species richness (Robinson *et al*. 1995). Meanwhile, a modeling approach employed by Goldstein *et al*. (2003) concluded that maximum richness of migratory species was achieved with an intermediate level of fragmentation, and Gates & Giffen (1991) showed the concentration of migratory birds at edges adjacent to ecotones (riparian zones). Goetz *et al*. (2010) also demonstrated the importance of structure and canopy height to explain migratory species richness. Overall, we hence note that numerous factors could explain the positive edge effect we found for short-distance migrants, and it would be an interesting perspective to study whether the matrix surrounding the forest patch may drive this edge effect. It would be also interesting to test whether differential habitat selection between migratory and resident birds could be used as a proxy for evaluating impacts of habitat fragmentation (Fahrig 1997, Fahrig 2003, Ribeiro *et al.* 2009, Lindenmayer & Fischer 2013).

### *Temporal dynamics of resident and migratory birds*

We found that the relationships between environmental variables and abundance of residents and long-distance migrants changed along the breeding season, while relationships between environmental variables and short-distance migrants persisted. Moreover, abundance of short-distance migrants was stable during the breeding season, while abundance of residents decreased at the last month of the breeding season and abundance of long-distance migrants increased from the second month. Thus, these results suggest a temporal dynamics of resident and migrant bird distribution, which could explain their spatial partitioning at the scale of the entire breeding season as well as the spatial structure of entire bird community. Long-distance migrants arrived indeed in the forest patch later than residents and short-distance migrants, in particular because presence of residents within the forest patch could be quite continuous during the year. Overall, distribution patterns of residents were closer to distribution patterns of short-distance migrants than those of long-distance migrants. Therefore, long-distance migrants might not find the same availability of habitats, and nested in zones less occupied by residents and short-distance migrants. An opposite result was found at inter-patch scale by Mönkkönen *et al.* (1990) and Thomson *et al.* (2003), who found the existence of an heterospecific attraction resulting in migratory species choosing habitat patches with many resident species, whose presence is interpreted as a signal of high habitat quality. Overall, if it had already been shown that habitat preferences of bird communities could vary seasonally between breeding season in spring and the beginning of autumnal migration (Murcia 1995, Griffis-Kyle & Beier 2005, Böhm & Kalko 2009, Keller *et al.* 2009, Naoe *et al.* 2011), no study had yet taken into account intra-season dynamics of bird distribution and the role of functional groups of migratory and resident birds in this dynamics. Thus, our results are novel and highlight the importance of accounting for spatio-temporal distribution patterns at fine scale.

## CONCLUSION

Our study showed at intra-patch scale that environmental variables (distance to edge, deciduous tree cover, elevation, coppice cover) drove individual bird species distribution as well as bird community indicators (abundance, diversity, evenness). Moreover, abundances of residents, short-distance migrants and long-distance migrants were differently related to environmental variables, in particular in regard to distance to forest edge, tree density, coppice cover and elevation. We also found that spatial distribution of bird species changed during the breeding season, depending on the migratory status of species. Specifically, we observed that, within the breeding season, distribution patterns of short-distance migrants were closer to distribution patterns of residents than to distribution patterns of long-distance migrants. Overall, long-distance migrants arrived later than residents and short-distance migrants in the breeding season, and it might explain the spatial partioning we observed between resident and migrant birds as well as the structure of the entire bird community: long-distance migrants might not find the same availability of high quality habitats, and might be forced to fall back on still available or low quality ones. These results show the importance of taking into account functional traits of bird species, especially migratory status, and intra-season temporal dynamics to study and understand the distribution patterns of bird communities. Such results may have implications for forest management, to optimize species assemblages and hence the conservation of avian biodiversity in temperate forest environments.

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## TABLES

**Table 1.** Environmental variables influenced bird community indicators. Summary of the best mixed models explaining each indicator of bird community by environmental variables. The effect of each significant fixed variables is indicated with its standardized regression coefficient and significance (*: $P<0.05$; **: $P<0.01$; ***: $P<0.001$) and the random effect is also indicated when significant (see Methods for model construction). N is the whole sample size and Adj-R² is the adjusted R-squared. Diversity is evaluated by the Shannon index.

| Bird community indicator | **Effect of environmental variables** | | | | | | | | | N | Adj-R² |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | distance to edge | coniferous | deciduous | elevation | heterogeneity | basal area | coppice | Random effect (month) Inter: lower/estimate/ upper | Random effect (month) Intra: lower/estimate/ upper | | |
| *Abundance* | **-0.30*** | | **0.32*** | | | | **-0.32**** | 0.1/0.4/1.2 | 0.8/0.9/1.1 | 87 | 0.21 |
| *Diversity* | **-0.38**** | | **0.36**** | | | | **-0.35**** | | | 87 | 0.12 |
| *Evenness* | | | | **-0.23*** | | | | | | 87 | 0.05 |
| *Residents* | | | | **-0.42***** | | | | 0.1/0.3/1.1 | 0.7/0.9/1.0 | 87 | 0.27 |
| *Short-distance migrants* | **-0.46***** | | | | | **-0.42***** | **-0.47***** | | | 87 | 0.26 |
| *Long-distance migrants* | | | | **0.32***** | | | | 0.2/0.6/1.8 | 0.7/0.8/0.9 | 87 | 0.45 |

**Table 2.** Relationships between environmental variables and short-distance migrants persisted along the breeding season, while relationships between environmental variables and abundances of residents and long-distance migrants changed. Summary of the best multiple linear models explaining abundances of residents, short-distance migrants and long-distance migrants by environmental variables, at the three months of the breeding season. The effect of each significant variables is indicated with its standardized regression coefficient and significance (*: P<0.05; **: P<0.01; ***: P<0.001). Other model parameters are the degree of freedom (Df), the F statistic (F), the *P*-value (*P*), and the adjusted R-squared (Adj-R²).

| | | **Effect of environmental variables** | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Abundance of | Month | distance to edge | coniferous | deciduous | elevation | neterogeneity | basal area | coppice | Df | F | *P* | Adj-R² |
| Residents | *April* | | | | **-0.59*** ** | | | | 27 | 14.6 | <0.001 | 0.33 |
| | *May* | **-0.37*** | | **0.86*** ** | | | | **-0.44*** | 25 | 6.7 | <0.001 | 0.38 |
| | *June* | | | | | | **0.37*** | | 27 | 4.2 | <0.05 | 0.10 |
| Short-distance migrants | *April* | **-0.57** ** | | | | | **-0.60** ** | **-0.50*** | 25 | 6.0 | <0.01 | 0.35 |
| | *May* | **-0.89** ** | | **0.54*** | | **-0.65*** | | **-0.37*** | 24 | 3.5 | <0.05 | 0.26 |
| | *June* | **-0.42*** | | | | | **-0.38*** | **-0.57** ** | 25 | 3.4 | <0.05 | 0.21 |
| Long-distance migrants | *April* | **0.61*** | **0.41*** | | | **0.70*** | | | 25 | 2.6 | <0.05 | 0.15 |
| | *May* | | | | **0.42*** | | | | 27 | 5.9 | <0.05 | 0.15 |
| | *June* | | | | **0.68*** ** | **0.30*** | | **-0.43*** | 25 | 6.4 | <0.001 | 0.37 |

## FIGURES CAPTIONS

**Figure 1.** Localisation of the study area and positions of the 29 bird point counts (500 m square grid), with (a): Elevation data and (b): Areas with dominant deciduous or coniferous tree communities.

**Figure 2.** Environmental variables drove individual abundance of bird species. PC1/PC2 co-inertia plane with projection of species (italics) and environmental variables (bold). Correlation coefficient=0.50, *P*=0.001 and total inertia=61.7%. Species codes: Frco: *Fringilla coelebs*; Erru: *Erithacus rubecula*; Trtr: *Troglodytes troglodytes*; Tume: *Turdus merula*; Phco: *Phylloscopus collybita*; Copa: *Columba palumbus*; Syat: *Sylvia atricapilla*; Sieu: *Sitta europaea*; Cebr: *Certhia brachydactyla*; Tuph: *Turdus philomelos*; Paca: *Parus caeruleus*; Tuvi: *Turdus viscivorus*; Dema: *Dendrocopos major*; Cocor: *Corvus corone*; Pama: *Parus major*; Cuca: *Cuculus canorus*; Oror: *Oriolus oriolus*; Phsi: *Phylloscopus sibilatrix*; Gagl: *Garrulus glandarius*; Papa: *Parus palustris*; Sttu: *Streptopelia turtur*; Rere: *Regulus regulus*; Antr: *Anthus trivialis*; Pivi: *Picus viridis*; Phph: *Phoenicurus phoenicurus*; Sybo: *Sylvia borin*; Prmo: *Prunella modularis*; Reig: *Regulus ignicapilla*; Deme: *Dendrocopos medius*; Stvu: *Sturnus vulgaris*; Drma: *Dryocopus martius* ; Aeca: *Aegithalos caudatus*; Pacr: *Parus cristatus*; Bubu: *Buteo buteo*; Acni: *Accipiter nisus*.

**Figure 3.** Influence of elevation on abundance of resident birds (filled triangles and full lines), short-distance migrant birds (empty points and fine-dashed lines) and long-distance migrant birds (filled points and large-dashed lines), over the entire breeding season. See Table 1 for models.

**Figure 4.** Influence of distance to edge and coppice cover on abundance of resident birds (filled triangles and full lines), short-distance migrant birds (empty points and fine-dashed lines) and long-distance migrant birds (filled points and large-dashed lines), for the three

months of the breeding season. Both variables are the most frequently significant among relationships between bird abundances and environmental variables at the three months of the breeding season. See Table 2 for models.

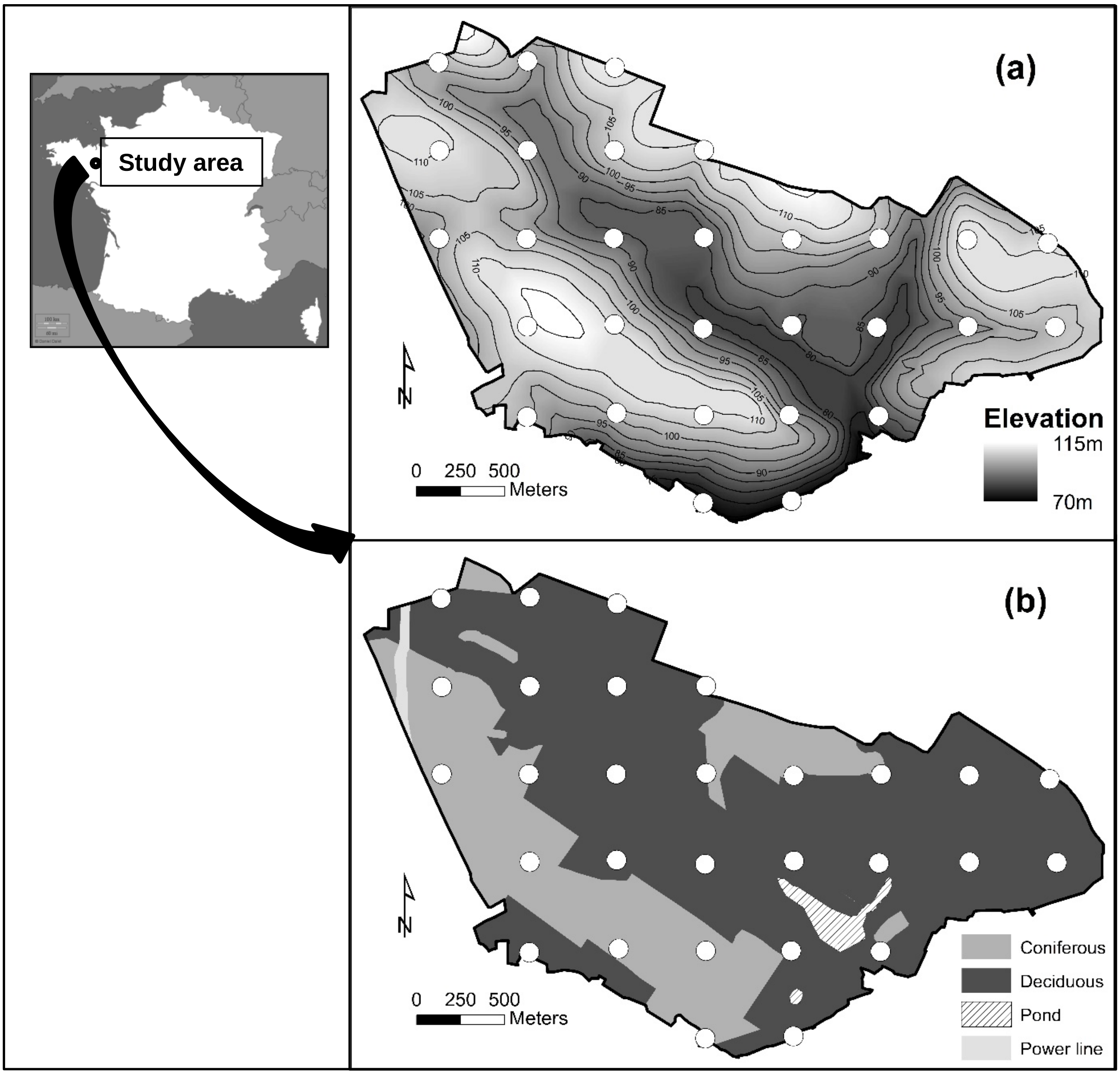

**Figure 1.**

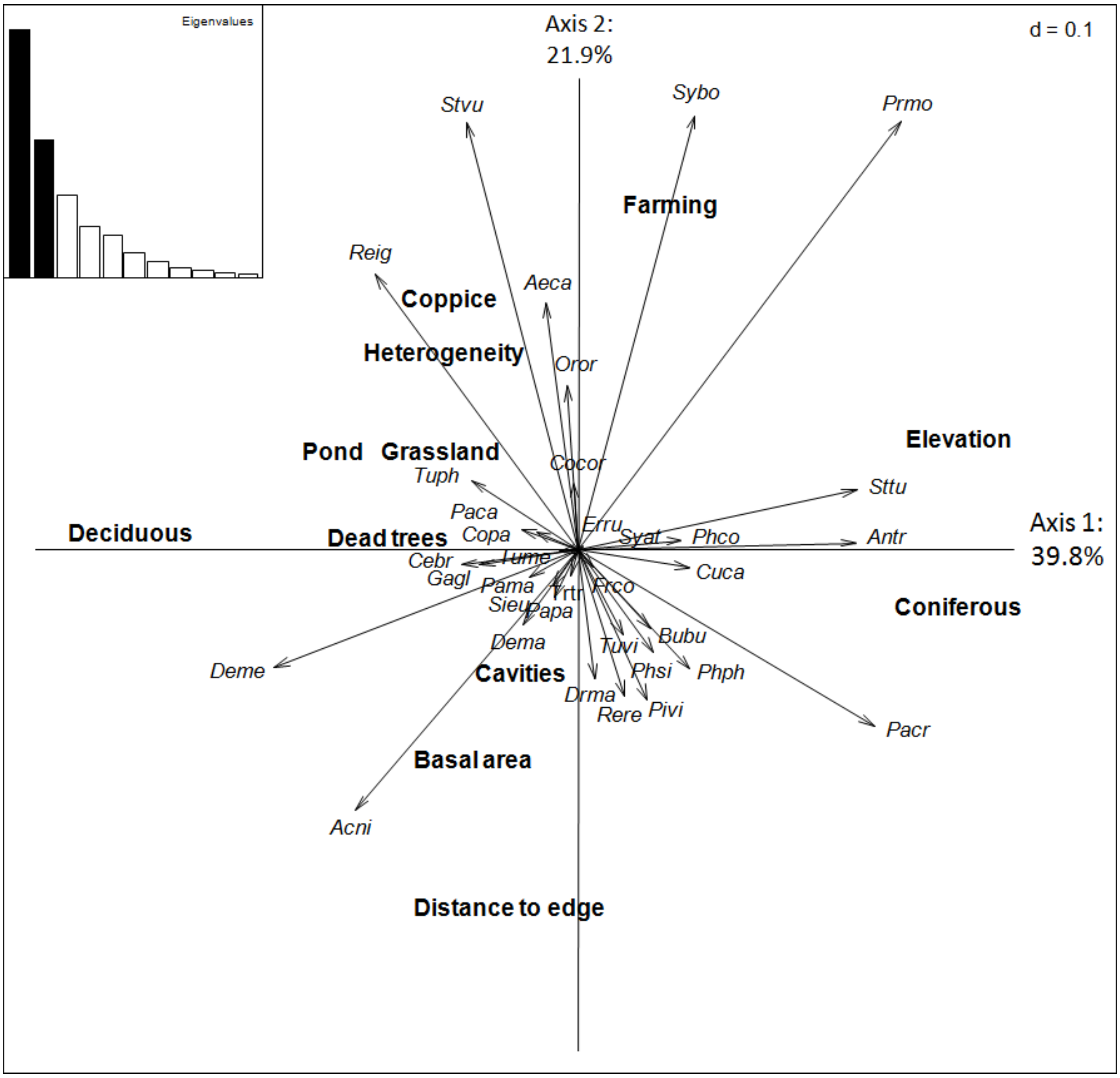
Eigenvalues
Axis 2:
21.9%
d = 0.1
Stvu
Sybo
Prmo
Farming
Reig
Coppice
Aeca
Heterogeneity
Oror
Elevation
Pond
Grassland
Cocor
Tuph
Sttu
Paca
Erru
Deciduous
Dead trees
Copa
Syat
Phco
Antr
Axis 1:
39.8%
Tume
Cebr
Gagl
Cuca
Pama
Frco
Trtr
Sieu
Papa
Coniferous
Bubu
Dema
Tuvi
Deme
Phsi
Phph
Cavities
Drma
Pivi
Rere
Pacr
Basal area
Acni
Distance to edge

**Figure 2.**

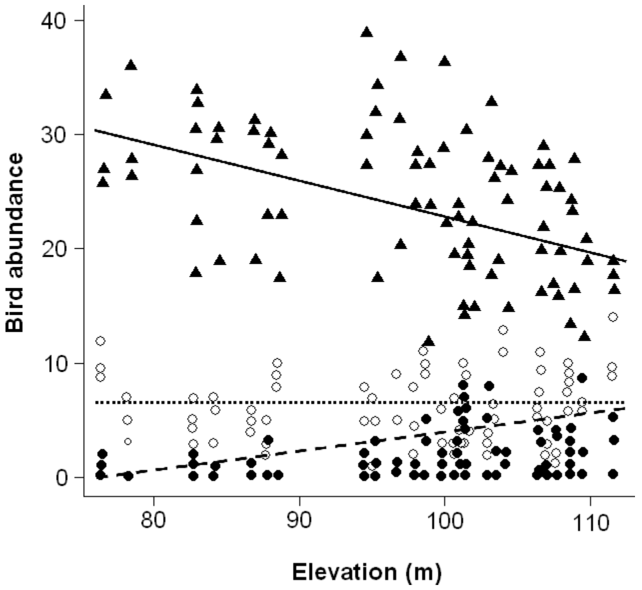

**Figure 3.**

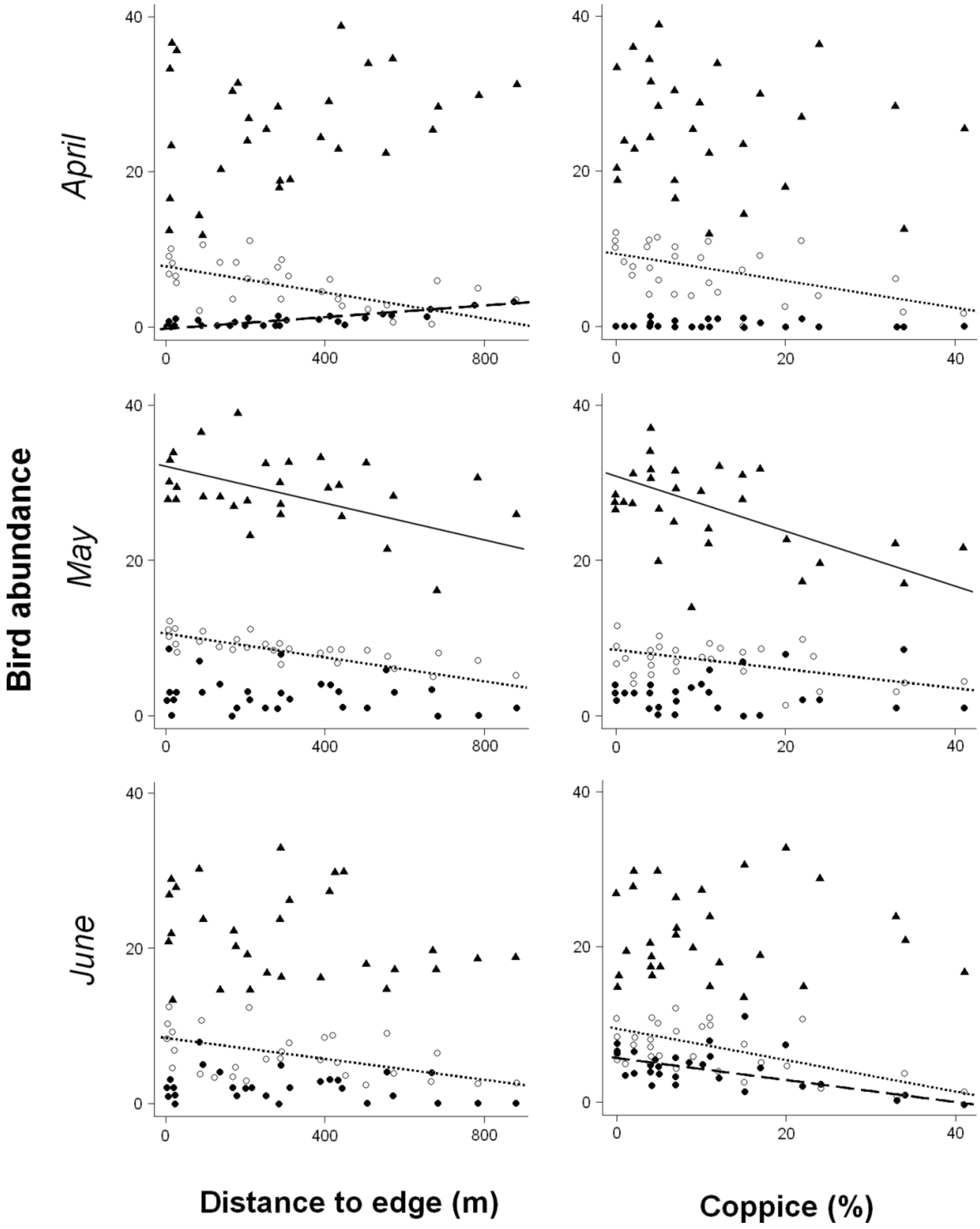
April
May
June
Bird abundance
0
20
40
0
400
800
0
20
40
Distance to edge (m)
Coppice (%)

**Figure 4.**