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**Assessing habitat/landscape predictors of bird diversity in managed
deciduous forests: a seasonal and guild-based approach**

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Abstract

In this study we focused on deciduous managed forests in northwest Italy and investigated relationships between bird diversity and forest descriptors both at the habitat and landscape level through a seasonal, guild-based approach. Birds were censused by point counts in randomly selected plots of 50 m radius. Each census plot was described in habitat structure terms by using the Bitterlich variable plot-radius method. Landscape metrics (both at *class-* and *landscape-level*, according to Fragstats' terminology) were measured within 500 m radius circle of each plot using an existing GIS database. We first identified specialist and generalist species according to the presence/absence of each species in relation to habitat structure measurements using generalized additive models (GAMs), then we tested for the effects of habitat and landscape variables on guild parameters (namely, bird species richness, Shannon diversity and abundance) using generalized linear models (GLMs). Our analyses showed that several habitat and landscape predictors affected bird diversity. However, in general, guild parameters relative to specialists were especially influenced by oak biomass (a habitat predictor) and oak core area (a *class-level* predictor) irrespective of the season, while parameters of generalists were influenced by oak core area in winter and perimeter/area ratio of oak patches in spring. *Landscape-level* predictors significantly affected winter

bird abundance only. Results clearly showed that the retention of native oaks both at the habitat and the landscape level is the key-factor for the conservation of diversity of specialist bird species in deciduous, originally oak-dominated woods. Results also suggest that studies focusing on different periods should be preferred to mono-season surveys and that a guild-based approach should be preferred to an holistic one taking into account all species.

Keywords

bird diversity, deciduous forest management, seasonal differences, black locust, oak, habitat, landscape, specialists, generalists, diversity conservation

Introduction

Forest management focused for a long time on wood production, with little consideration given to other values in forest ecosystems. Recently, however, the conservation of forest biodiversity has started to take into account sustainable forest ecosystem management (DeGraaf and Miller, 1996; Angelstam and Pettersson, 1997). In this framework, the effect of forest management on birds is a relevant topic. The assessment of the impact of forestry practices on bird communities may be considered as a multi-level task, relying on different spatial, seasonal and compositional levels of analysis.

Forestry practices may cause modifications at the habitat level. It is well known that changes in habitat structure (e.g. tree height, trunk diameter, tree density, foliage height profile, amount of snags and downed woody material, etc.) and tree species composition due to forest management can result in changes in composition of avian communities and in the abundance of many bird species (Welsh, 1987; Helle and Mönkkönen, 1990; Thompson et al., 1999).

Man-induced forest changes at the landscape level, especially habitat loss and fragmentation, are also major threats to forest biological diversity (Heywood, 1995; Stanners and Bourdeau, 1995; Dudley et al., 1996). Many studies have found bird populations to display sensitivities to fragmentation and shrinking forest patch size (Blake and Karr, 1987; Van Drop and Opdam, 1987; Thompson et al., 1999; King and DeGraaf, 2000). Changes in land use and landscape pattern configuration (including patch size and shape, distance between patches, etc.) have been shown to affect the number of bird species living in a forest (Freemark and Collins, 1992; Villard et al., 1999; Vander Haegen et al 2000; Santos et al., 2002), with a concomitant loss of native biodiversity and ecological integrity (Noss, 1993a, b; Noss and Cooperrider, 1994).

To assess the impact of forestry practices on birds, seasonal changes in the composition of local communities should also be taken into account. While most studies exploring the effects of habitat and/or landscape changes on forest avian communities dealt with breeding birds, surprisingly little attention was given to wintering ones (Laiolo et al., 2003). Winter is a critical period for most birds (Graber and Graber, 1979; Spencer, 1982), given that winter habitat availability may affect the occurrence and abundances of many species, thus conditioning their chances of survival until the breeding period (Telleria and Santos, 1995; Donald et al., 1997; Siriwardena et al., 1998; Telleria et al., 2001).

A further problem regards community composition. Studies on bird communities generally focus on parameters (e.g. abundance, species richness, diversity) which are derived from the whole set of species dwelling in the forest ecosystem. However, the holistic approach may be incongruous because species may react differently to the same environmental factors. Therefore, communities are sometimes split into guilds, which group animals according to their eco-ethological characteristics (Severinghaus, 1981; Brooks et al., 1998; O'Connell et al., 2000). To avoid losing the opportunity to compute several community parameters due to excessive splitting (computing species richness and diversity for a two-

specie guild is meaningless), a moderate splitting may be a valuable trade-off. One may focus, for instance, on habitat generalist species, which are able to thrive in a wide variety of habitats, and/or on habitat specialist species, which can only thrive in a narrow range of forest conditions. Guild-based results may also reflect biological integrity of forest ecosystem, which refers to a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates, under little or no influence from human actions (Angermeier and Karr, 1994).

Changes in habitat structure and composition, habitat loss and fragmentation due to silvicultural practices have occurred over much of the hill and lowland deciduous forests in northern Italy, where second-growth vegetation has replaced most of the original habitats. Here human pressure has resulted in severe cutting of forests to gain space for agriculture activities and for silviculture, with the following loss and fragmentation of forest, and the establishment of the black locust *Robinia pseudoacacia*, favoured by man because of its fast growth and good fuel-wood qualities.

We studied forest bird communities of deciduous forests of northwest Italy in spring and winter focusing upon guilds of specialist and generalist forest bird species, which were identified on the ground of their association with habitat structure variables. Relationships between birds and forest descriptors were investigated both at the habitat and landscape level. We first addressed birds-habitat relationships by means of habitat structure measurements. Then we investigated bird guild-landscape relationships using GIS techniques at two levels (i.e. *class-* and *landscape-levels*) at a landscape meso-scale (buffers of 500 m around the plot).

Through this multi-level approach we intended: i) to detect patterns of co-variation between guild parameters (species richness, diversity and abundance) and habitat and landscape variables over different periods (i.e. spring and winter) and ii) to single out and propose forestry management practices which are ecologically sustainable in that they warrant the preservation of local forest bird diversity and, concurrently, of forest integrity.

Methods

Study Area

The study was carried out in winter 2004-2005 and 2005-2006 and spring 2005 and 2006 in deciduous forests (397,61 km²) scattered in the Asti province, Italy (Fig. 1). The area is a hilly region (110-330 m a.s.l.), characterized by a sub-continental climate with Mediterranean influence. The most common forest management system is coppice, that produces patches at different growth stages, often grown with scattered single-stem trees or standards (mostly 80-100 years old oaks), which are fallen on a longer rotation time. Here human activities have always had a severe impact on forests, which have been harvested since the XVII century. However, in recent years the abandonment of agricultural land has partly favored a reforestation process, contributing to the spread of the black locust. Forest patches are dominated by 5-25 years old black locusts (73.71 % forest cover), oaks *Quercus petraea*, *Q. pubescens*, *Q. cerris* and *Q. robur* (14.47 % cover), sweet chestnuts *Castanea sativa* and poplars *Populus ssp.* (mostly in form of plantations). Oaks occur both as scattered standards in black locust woodlots and as associations (*Phytospermo-Quercetum petraea*, *Polygonato multiflori-Quercetum roboris*, *Querco-carpinetum*). The local forest landscape may be described as a rather continuous black locust matrix with interspersed single oak standards and oak-dominated internal patches.

Bird survey

Birds were surveyed using point counts (Bibby et al., 2000) in randomly selected plots of 50 m radius (0.8 ha) in forest stands dominated by black locusts or oaks. Observations were carried out in the morning, about four hours after sunrise. At the end of 10-min. sampling period, the observer (EC) also walked across the circular plot to detect birds that were not singing or flying during the point count to maximize

detections. Over-flying birds (i.e. those that did not land in trees or on the ground) were not considered. Each census plot was visited twice per season, from December to February in winter and from April to June in spring; the largest values from the two censuses for each season were used as a measure of bird species abundance per plot. Overall 200 plots were visited (94 in 2004-2005 and 106 in 2005-2006). The exact location of plots was established in the field by means of a global positioning system (GPS), Garmin eTrex® Navigator (Garmin Corporation, Olathe, KS).

Habitat

Each census plot was described in habitat structure terms. Measurements were made between the first and the second census visit, with the vegetation plot centered in the avian census plot. At each point we described the vegetation structure by using the Bitterlich variable plot-radius method (Bitterlich, 1947 and 1948). For each tree selected we measured the following variables: diameter of the trunk at breast height (DBH, in m), tree height (TH, in m) and canopy height (CH, in m) using an hypsometer (Suunto, Finland), under-storey density (the distance among the closest shrubs was paced in meters; the inverse gave the measure of density USD); these measurements were then summarized as mean values per plot. The variability in canopy profile and in trunk diameters (CVH and CVD) was estimated as the coefficient of variation ($=SD/mean*100$) of height and diameter measurements. For each plot we also estimated the number of trees per hectare (NT/ha). The national forest inventory double entry tables (Castellani et al., 1984) were used to calculate the volume of biomass for each tree species present from which the total volume (BV, in m³) and the relative volume percentage of each tree species (QB for oak, BLB for black locust and OB for volume of other trees) were derived. The percentage of ivy cover on the ground and on the trees and the volume of standing dead trunks were also subjectively assessed and recorded.

Landscape

Thirty-two landscape metrics were measured within a 500 m radius circular buffer around each plots using an existing GIS database (IPLA - Regione Piemonte 2005a,b) using ArcView 9.1 (Esri, 2004).

On the ground of preliminary analyses, we estimated that a 500 m radius was representative of diversity of habitats suitable for most wintering and breeding forest bird species in our study area. Due to the focus on forest birds, only landscape configuration variables of forests were assessed; non-forest habitat types were considered as background. We converted our maps to rasters selecting a cell size of 10 m which was appropriate to the scaling of our maps (Tobler, 1988). Forest patches were classified according to 3 habitat types (or classes): oak-dominated stands, black-locust-dominated stands and other stands. Fragstats 3.3 (Mc Garigal et al., 2002) was used to calculate landscape variables (or metrics) describing forest fragmentation. Eight *class-level* metrics and eight *landscape-level* metrics (in Fragstats' terminology) were considered (Appendix 1). *Class-level* metrics were habitat type-specific (i.e. they referred to oak-dominated stands or to black-locust dominated stands etc.), while *landscape-level* were not. To avoid any nomenclatorial confusion with the term "landscape", hereafter we referred to the above metrics by using italic types. *Class-level* metrics were calculated for each habitat type, therefore giving rise to twenty-four measurements (8 metrics per 3 habitat types). To avoid problems due to Modifiable Areal Unit Problem (MAUP) that can cause spurious results in GIS based landscape analyses (since landscape analyses are sensitive to extent and grain size (Wu, 2004)), we used the same extent and grain size for all sites, and used the original digital maps at the resolution the data were collected (Jelinski and Wu, 1996). We also used a combination of landscape metrics to describe buffers around plots, minimizing problems unique to each index (Li and Wu, 2004). Buffers were categorized into habitat types that were relevant to both management and our study

Data analysis

Spatial autocorrelation among plots was tested by comparing guild parameters and UTM coordinates of each plot with Mantel test (Fortin and Gurevitch, 1993; Legendre, 1993; Koenig and Knops, 1998; Koenig, 1999). Mantel test evaluates the similarity between an ecological distance matrix and a geometric distance matrix. If spatial autocorrelation exists, then the closer the points are in geometric space, the more similar should be the values of the community parameters. We used Monte Carlo simulations to test the hypothesis that there was no correlation between bird community parameter matrix and UTM coordinate matrix: P values were based on the proportion of 9999 Monte Carlo simulations. Mantel test was performed using PC-ORD (McCune and Mefford, 1999). We found no spatial autocorrelation ($r = 0.04$, $p = 0.10$) among guild parameters of closer plots.

Avian guild diversity was described for each census plot in terms of bird species richness (R), Shannon diversity [$H' = -\sum p_i \ln p_i$, where p_i is the relative frequency of species i (Shannon and Weaver 1949)] and abundance of individuals (N).

Since the structural habitat variables are intrinsically correlated, much of the information in one or more of these can be redundant and thus the results of analyses based on these raw predictors may be ambiguous (Jongman et al., 1995). Principal Component Analysis (PCA: Gaunch, 1984) was chosen to minimize the effects of multicollinearity and to reveal patterns in the data for habitat structure using standardized data (zero mean and unit standard deviation) (Legendre and Legendre, 1998). PCA was computed with SPSS 13.0 for Windows (SPSS Inc., 2003).

We utilized generalized additive models (GAMs) (Hastie and Tibshirani, 1990) to test for the effects of habitat structure (three scores of PCA) on presence/absence of each bird species with a frequency of occurrence $> 1\%$ in each plot with binomial errors and logit link. Compared with GLMs, the main difference is that GAMs are data-driven rather than model-driven. This nonparametric category of models allows determination of the shape of the response curves from the data instead of fitting an *a priori* parametric model which is limited in its available shape of response (Wood and Augustin, 2002).

GAMs were performed using the R package and mgcv library (R Development Core Team, 2005), specifying a binomial family with a logistic link function. The default cubic smoothing spline method with 4 degrees of freedom was chosen to smooth the three PCA variables.

We used P-values ($p < 0.1$) to classify species that were positively correlated with PC1 (a gradient of forest age, see below) and/or negatively correlated with PC3 (shrub density) derived from structure variables as “specialists”, and those having negative correlation with PC1 or positive correlation with PC3, or no correlation at all, as “generalists”.

Many landscape metrics calculated with Fragstats were also correlated. In this case, given that PCA generated ambiguous derived components and that correlated metrics had different biological meaning (i.e. edge, area, core area etc.), we performed a different variable reduction procedure before proceeding with the statistical modeling phase. In order to avoid multicollinearity among variables we first examined all pairwise correlations to identify correlated pairs ($r > |0.7|$). Then, following Riitters et al. (1995), one variable was selected to represent each group of highly correlated variables, selection criteria including the degree of normality and our subjective estimate of interpretability. This procedure reduced the number of *class-level* variables from 24 to 10 and that of *landscape-level* variables from 8 to 5.

Since a preliminary analysis of the data showed that variables had only linear contributions in models, we used GLM to test for the effects of uncorrelated habitat variables (percentage of ivy at ground, percentage of ivy on trees, dead trees biomass, oak biomass, black locust biomass, biomass of other trees) and of landscape variables (explanatory variables) on bird species richness, diversity and abundance of specialist and generalist guilds (response variables) in winter and spring using a backward stepwise function; data on species diversity were normally distributed and a normal distribution of error assumption with an identity link was applied; abundance and species richness instead are count data, and a Poisson distribution was assumed, with means determined by a log link function to the covariates.

Finally, significant habitat, *class*- and *landscape-level* variables were merged to carry out GLM which intended to point out the most important habitat and/or landscape predictors of bird diversity. Landscape and habitat variables were log-transformed [$y = \log(x + 1)$] was used to select the most appropriate models, i.e. the best fit to the available data set. Akaike's Information Criterion (AIC: Akaike, 1973) was used to select the most appropriate models, i.e. the best fit to the available data set. AIC is based on the principle of parsimony and helps to identify the model that accounts for the most variation with the fewest variables: the model that best explains the data is that with the lowest AIC. This information criterion is one of the most powerful approaches for model selection from a set of alternative plausible models and it solves the problems of stepwise model selection because no sequential statistical test is conducted (Burnham and Anderson, 1998).

Results

1) Community composition

Overall, 2404 individuals from 32 species were sampled in winter and 1588 individuals from 33 species were sampled in spring (appendices 3 and 4, respectively). In winter Robin *Erithacus rubecola* and Great Tit *Parus major* were the most common species, with frequencies of occurrence higher than 60%. Blackbird *Turdus merula*, Blue Tit *Parus caeruleus*, Marsh Tit *Parus palustris*, Wren *Troglodytes troglodytes* and Chaffinch *Fringilla coelebs*, were also rather common, with frequencies comprised between 40 and 50%, followed by Great spotted woodpecker *Picoides major*, Jay *Garrulus glandarius* and Nuthatch *Sitta europaea* (frequencies of occurrence between 30 and 40%). In spring Blackbird was the most common species, with a frequency of 65.5%; Great tit, Robin and Blackcap *Sylvia atricapilla* were also rather common

with frequencies comprised between 50 and 60 %, followed by Great Spotted Woodpecker, Blue tit and Jay, with frequencies comprised between 30 and 40 %.

2) Species ecological classification

GAMs were used to test for the effects of habitat structure variables (three scores of PCA) on presence/absence of each bird species. The first three principal components of the PCA (PC1, PC2, PC3) accounted for 79.96 % of variance in the habitat structure matrix, with eigenvalues > 1. Mean tree diameter and height, total biomass volume and canopy height showed a positive correlation with PC1, while the number of trees per hectare was negatively correlated with PC1, suggesting a gradient of forest age, from young to old stands. Coefficient of variation of tree height and diameter provided major positive loadings on PC2, shrub density showed a positive correlation with PC3 (appendix 2).

In winter ten species were positively correlated with PC1 and were classified as specialists; nineteen species were classified as generalists (one was positively correlated with PC3, and 17 species showed no significant correlation). In spring thirteen species were classed as specialists (eleven showed positive correlation with PC1, one showed negative correlation with PC3 and one a positive correlation with PC1 and negative one with PC3) and sixteen as generalists (no significant correlation with PC scores). The results of GAMs of species presence/absence in winter and spring in relation to habitat structure are shown in appendices 3 and 4, respectively.

Typical forest specialist species (classified in this guild both in winter and in spring) comprised arboreal birds like Great and Lesser spotted woodpecker *Picoides minor*, Short-toed treecreeper *Certhia brachydactyla*, Nuthatch, Jay and Blue tit.

3) Predictors of species diversity

a) Habitat

All diversity parameters (species richness, Shannon diversity and abundance of individuals) relative to specialists were positively correlated with oak biomass in both seasons; two parameters (i.e. species diversity and abundance) in spring and one (abundance) in winter were also negatively correlated with black locust biomass. Parameters relative to generalists, with the only exception of abundance of individuals (which was negatively correlated with black locust biomass in winter), were not correlated with any habitat predictor. Results of habitat analyses relative to wintering and breeding guilds are shown in tables 1 and 2, respectively.

b) Landscape

At the *class-level* all winter parameters of both specialist and generalist species were best modelled by a combination of variables that included oak core area, which was positively associated with bird diversity measures. Spring parameters of specialists showed the same trend, while spring parameters of generalists were positively associated with the mean of perimeter-area ratio of oak patches (oak PARA).

At the *landscape-level*, parameters of generalists were negatively correlated with the mean of perimeter-area ratio of all patches (LAND_PARA) in winter, and with the total amount of core area in the landscape (LAND_CORE) (with the exception of species richness) in spring. Most of the parameters of specialists (two in spring and two in winter) were positively correlated with the total perimeter of patches (LAND_TE). Results of landscape analyses relative to wintering and breeding guilds are shown in tables 3 and 4, respectively.

c) Habitat plus landscape

Habitat and landscape variables which significantly entered previous models were analysed together to look for the strongest predictors of bird diversity. All parameters relative to specialists were definitely and positively associated with oak core area (a *class-level* predictor) and/or oak biomass (a habitat

predictor). All parameters relative to generalists were positively associated with oak core area in winter and with oak PARA in spring (with the exception of abundance). Virtually all *landscape-level* predictors (a part from LAND_PROX) significantly influenced winter bird abundance only. They were: LAND_TE, which was positively associated with abundance of specialists, LAND_PARA, negatively associated with both specialists and generalists, LAND_SHAPE, negatively associated with specialists and the total amount of forest in the landscape (LAND_AREA), negatively associated with generalists. The results of GLMs run to test for the effects of habitat plus landscape predictors on guild parameters are shown in tables 5 (winter) and 6 (spring).

Discussion

Man-induced forest changes at the landscape level can promote loss of natural forest habitats and fragmentation (Palik and Engstrom, 1999), which are causes of the recent decline in biological diversity in many countries (Heywood, 1995; Stanners and Bourdeau, 1995; Dudley et al., 1996). In our study area, human pressure has resulted in severe cutting of forests to gain space for agriculture activities, with the following loss and fragmentation of deciduous forests. In addition, silvicultural practices favoured black locust (73.71% of forest cover), an alien species which has been established at the expense of native oaks. We focused on forest habitat only and found that changes in habitat and landscape structure and composition due to forest management result in complex, level-dependent changes in bird diversity (keeping with Thompson et al., 1999 and Laiolo et al., 2003) and that responses to such disturbances may be substantially different in different seasons and guilds. Results proved to be useful both to delineate appropriate methods for assessing forest bird diversity and to suggest better conservation strategies.

1) Effects of habitat and landscape

In general, guild parameters were found to be sensitive to just one or few habitat and/or landscape metrics. This suggests that bird diversity depends on precise predictors, thus supporting the data reduction procedure we performed. Moreover, it can be underlined that the biological meaning and/or the effect of the metrics is different. For example, the amount of forest cover in a buffer can vary regardless of the amount of edge length and two buffers with same forest extent can vary in number of patches, core area extent or perimeter/area ratio, depending on the arrangement of patches (Forman and Godron 1986).

a) Habitat

All diversity parameters of specialists, irrespective of the season, were positively correlated with oak biomass, whereas parameters of generalists were not influenced by such predictor. These results, in line with other studies which documented a positive relationship between bird richness, diversity, or abundance and measures related to biomass (Verner and Larson, 1989; Mills et al., 1991), emphasize differences between generalist and specialist species. It might be assumed that true forest specialists (Great and Lesser spotted woodpecker, Nuthatch, Short-toed treecreeper, Jay, Blue tit etc.) depend on food yielded by oaks, especially acorns and invertebrates of decaying wood (Lack and Lack, 1951; Moss, 1978; Ferry and Frochot, 1990; Helle and Mönkkönen, 1990). The effect of black locust biomass on guild diversity, albeit not always significant, was clearly negative. It is likely that this tree species does not yield enough food, probably because each individual tree supports less invertebrates due to its smaller volume, and/or because a rich invertebrate specialized wood fauna has not evolved yet (Laiolo et al., 2003).

b) Landscape

At the *class-level*, our results suggest that local guilds are affected by the spatial distribution of oaks in the landscape and that bird diversity, relative to specialists in both seasons and to generalists in winter, increases with increasing occurrence of oak patches with large core areas.

At the *landscape-level*, the existence of significant predictors of guild diversity (they were LAND_PARA and LAND_CORE for generalists and LAND_TE for specialists) seems to indicate that the geometry of patches matters *per se* (remind that *landscape-level* variables are independent of patch composition). Consider, as an example, LAND_TE, which measures edges between forest patches. In our area the increase of total edges mostly depends on the increase of adjacent, contiguous patches with different forest management. Forest edges have been commonly presumed to have deleterious biotic and abiotic consequences for the organisms that inhabit and breed in forest fragments (Murcia, 1995) but, it is likely that edges can be attractive for some species of birds (Galli et al., 1976). Results at the *landscape-level* might suggest that forestry diversification of patches *per se*, may be sustainable.

c) Habitat plus landscape

When we analyzed effects of habitat, *class-* and *landscape-level* metrics together, GLM analyses showed that the strongest predictors of local bird diversity were habitat and *class-level* metrics related to the presence of native oaks, i.e. oak biomass and oak core area. The presence of oaks was particularly important for specialist species, as outlined for local native tree species in previous works (Andr n, 1994; Price et al., 1999; Lee et al., 2002, Tubelis et al., 2007). *Landscape-level* predictors were certainly weaker since only winter bird abundance was significantly affected. All the above indicates that birds are primarily affected by the presence of certain tree species in terms of biomass and distribution and that, secondarily, they may be influenced by the shape of patches, irrespective of their tree composition. In general, the better performance of habitat and *class-level* with respect to *landscape-level* metrics may be explained by assuming that birds are more able to perceive the identity and characteristics of trees than abstract geometric characteristics of a patch.

Differences between guilds and seasons were confirmed because specialist parameters were positively associated with both metrics in both seasons, whereas generalist parameters were associated with oak core area in winter and oak PARA in spring.

Hence, our study confirms that forest integrity, that should be obtained through the maintenance of native tree species, is crucial to preserve bird diversity (Telleria and Santos, 1995; Doherty and Grubb, 2000; Turcotte and Desrochers, 2005).

2) Methodological and conservation implications

The seasonal and guild-based bird diversity pattern we depicted above deserves a serious methodological consideration. In winter both specialist and generalist species choose areas with large oaks; in this case, an holistic approach, which considers all species together, would be substantially correct. In spring, conversely, responses of specialists and generalists were different (the former guild was much more related to habitat and *class-level* metrics than the latter was) and an holistic approach would be probably incorrect, giving rise to spurious estimates.

Our seasonal guild-based approach may have relevant consequences for forest bird conservation as well. In general, results clearly demonstrate that the retention of native oaks both at the habitat and the landscape level is the key-factor for the conservation of diversity of specialist species in deciduous, originally oak-dominated woods. However, it should be emphasized that this simple forest management intervention, although positively affecting specialists in both seasons and generalists in winter, does not seem to affect generalists in spring.

Our guild approach goes beyond total diversity to the more informative structural and functional diversity of guilds. High values of diversity parameters of forest specialist species are likely more indicative of habitat availability and quality than would be the case for overall community (Bishop and

Myers, 2005). Plots with high bird diversity values are also characterized by high values of oak-related habitat and *class-level* predictors, which reflect a higher ecological integrity.

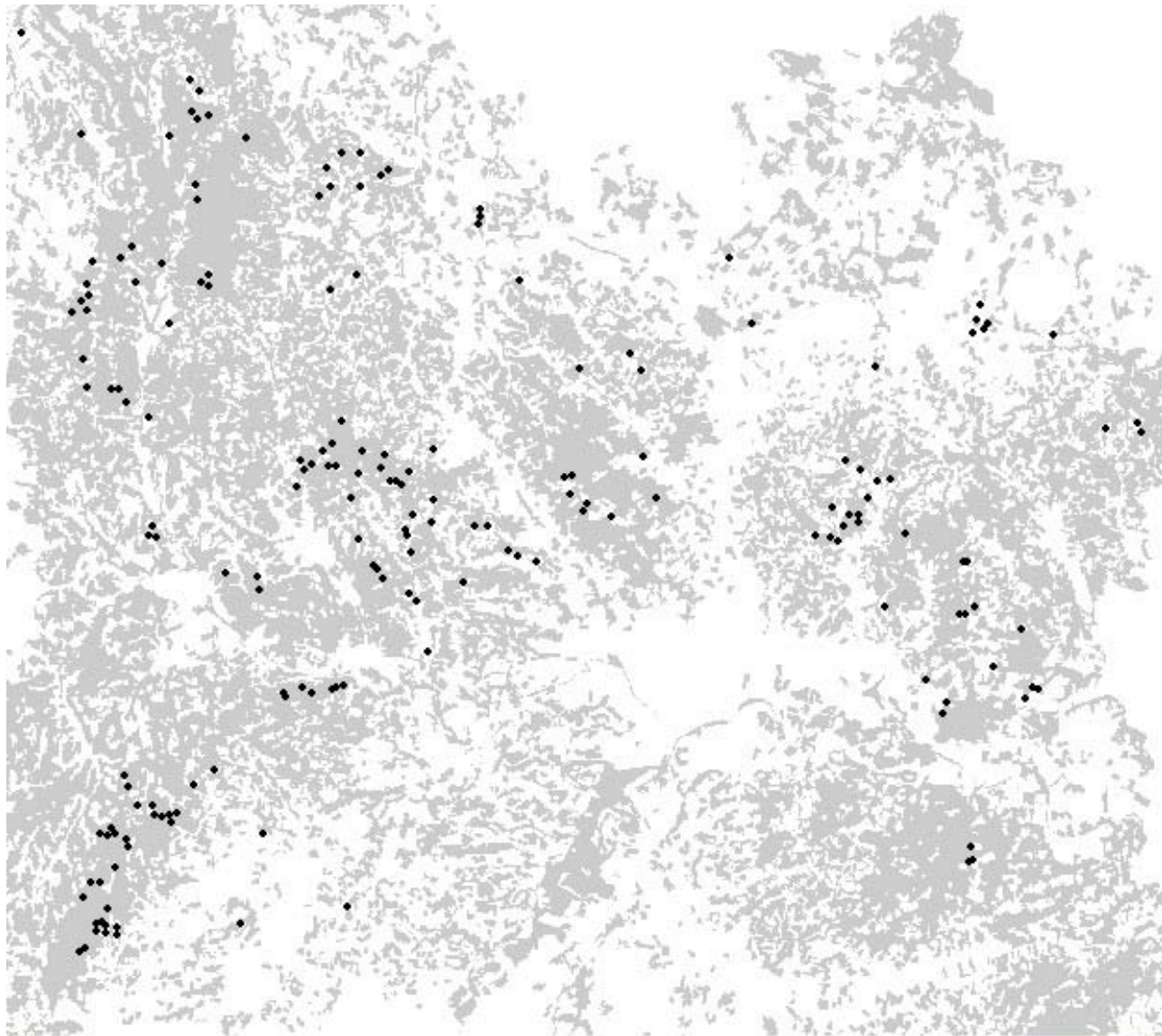
Introduced, non-native vegetation can alter community composition and nesting success of birds (Wilson and Belcher, 1989; Schmidt and Whelan, 1999). In our study area, ecological integrity is particularly threatened by forest management which favours the spreading of the black-locust, an introduced tree which replaces native habitats and severely harms native bird communities (Hruska, 1991, Sjoberg and Dannel, 2001, Zurita et al., 2006). Protecting biodiversity in fragmented landscapes requires substantial conservation and ecosystem restoration efforts (Young 2000; Lindenmayer et al., 2003). We admit that logging can contribute to increase the overall bird diversity introducing clearcuts and several stand age successions (Keller et al., 2003, Loehle et al., 2005). However, given that our results suggest the overall diversity may be misleading in a forest context and that forest changes induced by logging are substantially negative when favouring the black locust, we believe that the preservation of forest integrity should be a priority, at least in our study area. In forest management terms, this means that black locust harvesting may be tolerated on condition that old, large, native oaks are retained in all local stands, contributing to landscape connectivity and thus assuring movements and foraging resources through the landscape (Fischer and Lindenmayer, 2002).

As the effects of logging and forestry practices can vary throughout the year, studies focusing on different periods should be preferred to mono-season surveys (Laiolo et al., 2004). This would sharpen the precision with which it is possible to prescribe, in detail, how to conserve biodiversity in managed environments, and a combined strategy of protection, restoration and management of forests could be undertaken in order to include opportunities for sustainable logging that preserve forest integrity.

Acknowledgement

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1:160.000

Legend

Land use classes



-  Agricultural and urban areas
-  Forest patches

Fig. 1. Map of the study area with geographical location of plots (black dots). Forest area in light grey and agricultural and urban areas in white.

Table 1.

GLM of diversity, abundance and species richness of birds in winter in relation to habitat predictors. Only significant variables included in the best model (i.e. that minimizing AIC) are shown.

Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
Oak biomass	0.2723	0.0473	***	ns			
AIC = 318.34							
Abundance				Abundance			
Black locust biomass	-0.1195	0.0509	*	Black locust biomass	-0.1358	0.0308	***
Oak biomass	0.4192	0.0538	***				
AIC = 1137.4				AIC = 1288.60			
Species Richness				Species Richness			
Oak biomass	0.3913	0.0490	***	ns			

AIC = 763.16



Table 2.

GLM of diversity, abundance and species richness of breeding birds in spring in relation to habitat predictors. Only significant variables included in the best model (i.e. that minimizing AIC) are shown.

Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
Black locust biomass	-0.1388	0.0664	*	ns			
Oak biomass	0.2664	0.0608	***				
AIC = 280.79							
Abundance				Abundance			
Black locust biomass	-0.1329	0.0597	*	ns			
Oak biomass	0.4162	0.0626	***				

Other trees biomass	0.1373	0.0599	*
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AIC = 896.42

Species Richness

Species Richness

Oak biomass	0.3951	0.0718	***	ns
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Other trees biomass	0.1534	0.0696	*
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AIC = 747.15

Table 3

GLM of diversity, abundance and species richness of birds in winter in relation to landscape predictors (at *class-* and *landscape-level*). Only significant variables included in the best model (i.e. that minimizing AIC) are shown.

<i>Class-level</i>							
Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
Oak core area	0.6873	0.1719	***	Oak Core Area	0.4566	0.1209	***
AIC = 326.05				AIC = 220.02			
Abundance				Abundance			
Other trees core area	0.7970	0.1564	***	Total forest cover	-0.2342	0.1315	*
Oak SHAPE	0.5398	0.2161	*	Oak core area	0.6920	0.0831	***
Oak core area	0.9005	0.1065	***	Other trees PARA	-0.0575	0.0200	**

AIC = 1063.2				AIC = 1231.0			
Species Richness				Species Richness			
Oak core area	0.7727	0.1287	***	Oak Core Area	0.4829	0.1317	***
Oak PARA	0.1265	0.0371	***				
AIC = 813.12				AIC = 725.1			

<i>Landscape-level</i>							
Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
ns				LAND_PARA	-0.3200	0.1418	*
				AIC = 228.84			
Abundance				Abundance			
LAND_TE	1.9788	0.3760	***	LAND_PARA	-0.4118	0.1163	***
LAND_SHAPE	-5.7271	1.1319	***				
LAND_PARA	-0.7440	0.1899	***				
AIC = 1275.8				AIC = 1298			
Species Richness				Species Richness			
LAND_TE	1.3200	0.4184	**	LAND_PARA	-0.4173	0.1728	*

AIC = 845.7

AIC = 731.45

Table 4

GLM of diversity, abundance and species richness of breeding birds in spring in relation to landscape predictors (at *class-* and *landscape-level*). Only significant variables included in the best model (i.e. that minimizing AIC) are shown.

<i>Class-level</i>							
Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
Black locust Area	0.4299	0.1341	**	Oak PARA	0.0714	0.0267	**
Oak core area	0.8290	0.1849	***				
AIC = 317.2				AIC = 238.95			
Abundance				Abundance			
Oak core area	0.5463	0.1343	***	Oak PARA	0.0583	0.0282	*
Oak SHAPE	0.6136	0.2441	*				

AIC = 1015.6				AIC = 953.9			
Species Richness				Species Richness			
Oak core area	0.6172	0.1529	***	Oak PARA	0.0769	0.0359	*
AIC = 824				AIC = 723.5			

<i>Landscape-level</i>							
Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
LAND_TE	1.048	0.482	*	LAND_CORE	-0.2485	0.1095	*
AIC = 334.63				AIC = 234.23			
Abundance				Abundance			
LAND_PROX	0.1345	0.0582	*	LAND_CORE	-0.2857	0.1170	*
AIC = 1044.9				AIC = 952.16			
AIC = 1275.8				AIC = 1298			
Species Richness				Species Richness			
LAND_TE	1.5047	0.4433	***	ns			

AIC = 840.12

Table 5.

GLM of diversity, abundance and species richness of birds in winter in relation to best predictors of habitat structure, *class-* and *landscape-level*. Only significant variables included in the best model (i.e. that minimizing AIC) are shown.

Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	P
Species Diversity				Species Diversity			
Oak core area	0.4076	0.1732	**	Oak Core Area	0.4293	0.1210	***
Oak biomass	0.2402	0.0486	***				
AIC = 314.79				AIC = 218.46			
Abundance				Abundance			
Other trees core area	0.5577	0.1616	***	Oak core area	0.5622	0.0909	***
Oak core area	0.5554	0.1062	***	Other trees PARA	-0.0582	0.0201	**
LAND_TE	0.8827	0.3770	*	LAND_AREA	-0.2615	0.1319	*

LAND_SHAPE	-3.6077	1.1054	**
LAND_PARA	-0.4536	0.1732	**
Oak biomass	0.3854	0.0532	***

AIC = 1085.3

LAND_PARA	-0.3008	0.1183	*
Black locust biomass	-0.0896	0.0331	**

AIC = 1224

Species Richness

Oak core area	0.4610	0.1390	***
Oak biomass	0.3254	0.0530	***

AIC = 780.48

Species Richness

Oak Core Area	0.4398	0.1322	***
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AIC = 723.38

Table 6.

GLM of diversity, abundance and species richness of breeding birds in spring in relation to best predictors of habitat structure, *class-* and *landscape-level*. Only significant variables included in the best model (i.e. that minimizing AIC) are shown.

Specialists				Generalists			
Predictor	Beta	SE	p	Predictor	Beta	SE	p
Species Diversity				Species Diversity			
Black locust Area	0.5337	0.1244	***	Oak PARA	0.056	0.0275	**
Oak core area	0.5194	0.1639	**				
Black locust biomass	-0.2236	0.0676	**	AIC = 234.23			
Oak biomass	0.1549	0.0618	*				
AIC = 267.68							

Abundance				Abundance			
Oak core area	1.2528	0.5816	*	ns			
LAND_PROX	0.1500	0.0653	*				
Oak biomass	0.3787	0.0638	***				
Other trees biomass	0.1472	0.0616	*				
AIC = 887.9							
Species Richness				Species Richness			
Oak core area	0.3669	0.1488	*	Oak PARA	0.0769	0.0359	*
Oak biomass	0.3544	0.0720	***				
Other trees biomass	0.1721	0.0701	*				
AIC = 744.32				AIC = 723.5			

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