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# **Native oak retention as a key factor for the conservation of winter bird diversity in managed deciduous forests in northern Italy**

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## **Abstract**

Birds can serve as useful model organisms to investigate community level consequences of forestry practices. In this study we investigated the relationships between wintering bird communities and habitat and landscape characteristics of lowland managed forests in Northern Italy. This area is characterized by the spread of the black locust, an alien species that has been favored by forestry practices at the expense of natural oak forests. Birds were censused in winter by point counts in randomly selected plots of 50 m radius. We first addressed bird community–habitat relationships by means of habitat structure measurements, then we investigated bird community–landscape relationships by using GIS techniques. We used generalized linear models (GLM) to test for the effects of habitat and landscape variables on bird community parameters (namely bird species richness, diversity and abundance). Bird community parameters were influenced by oak biomass and tree age, and by oak area and core area, while the other forest habitat types showed less influence. In forest management terms, the main conclusion is that the retention of native oaks is the keyfactor for the conservation of winter bird diversity in local deciduous woods. At the habitat level black locust harvesting may be tolerated, provided that old, large, native oaks are retained in all local woodlots to preserve landscape connectivity and foraging resources. At the landscape meso-scale, large native oak patches, should be preserved or, where necessary, restored.

## **Keywords**

Bird community Forest cover Landscape pattern Oak Black locust Forest fragmentation Class and landscape-predictors Italy

## Introduction

Forestry practices are known to induce changes in habitat structure and composition and cause habitat loss and fragmentation (Palik and Engstrom 1999; Hunter 2000; Boutin and Hebert 2002; Lindenmayer et al. 2003; Monserud et al. 2007; Newton 2007). These effects are apparent in most of the hill and lowland forests of Northern Italy, where second-growth vegetation has replaced most of the original habitat. Here human pressure has led to extensive deforestation to make room for agriculture and forestry, with the consequent loss of forest habitat, fragmentation and the establishment of the black locust *Robinia pseudoacacia*, favoured by man because of its rapid growth and suitability as fuel (IPLA 2004a and b). In many areas, forest landscapes comprise a nearly continuous black locust matrix with interspersed single oak standards and oak-dominated internal patches; forests are surrounded by vineyards (especially in hilly areas) and crops (Correggia 2002).

Birds have often served as model organisms to investigate community level consequences of forestry practices (Bani et al. 2002). It is well known, for instance, 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 (Thompson et al. 1999; Laiolo et al. 2004a, b). In a bird diversity conservation framework, the preservation of old stands seems to be particularly desirable because they support more species and higher diversity values (MacArthur et al. 1966; Donald et al. 1997).

Besides modifying habitat structure, forest management and logging practices can contribute to landscape changes, promoting habitat loss and habitat fragmentation. Habitat loss has important negative effects on avian biodiversity (Schmiegelow and Mönkkönen 2002; Fahrig 2003; Lindenmayer et al. 2003). The effects of fragmentation are less univocal. However, when fragmentation exceeds a critical threshold (Andrén 1994), it may become a serious threat to biodiversity (Paton 1994; Chalfoun et al. 2002; Batáry and Báldi 2004). Forestry practices may also modify internal characteristics of patches (e.g. changes in tree species composition), inducing changes in landscape metrics (e.g. number of patches, patch area and perimeter, patch isolation, etc.), which are known to affect bird communities as well (Villard et al. 1999; Vander Haegen et al. 2000; Santos et al. 2002).

While most studies exploring the effects of habitat or landscape changes on forest avian communities have dealt with breeding birds, surprisingly little attention has been devoted to wintering birds (Laiolo et al. 2003; Bani et al. 2006). Winter is a critical period for many birds (Graber and Graber 1979; Spencer 1982), since winter habitat availability may affect the occurrence and abundances of many species, thus conditioning their chances of survival until the breeding season (Telleria and Santos 1995; Donald et al. 1997; Siriwardena et al. 1998; Telleria et al. 2001).

Habitat and landscape changes in North Italy are particularly worrying because they may lead to the loss of typical forest bird species, which may in turn compromise ecosystem functionality (Bani et al. 2002; Laiolo 2002; Laiolo et al. 2003; Bani et al. 2006) but no studies have been carried on in this area taking into account habitat and landscape effects on wintering bird communities. We investigated relationships between wintering bird communities and forest structure and composition in lowland forests of north-western Italy at both the habitat and landscape scales. Processes that modify the environment by changing habitat structure and landscape configuration are spatially nested (Cushman and McGarigal 2004a, b), and can be treated at different scales.

We surveyed birds by means of 50 m radius point counts and investigated bird community–habitat relationships by describing vegetation structure and bird community–landscape relationships using GIS techniques at two levels (i.e. class- and landscape-levels, see below) at landscape meso-scale (buffer of 1,000 m radius around the plot).

Through this approach focused on habitat and landscape, we intended: (i) to detect patterns of co-variation between winter community parameters (bird species richness, diversity and abundance)

and habitat and landscape variables, (ii) to single out and propose forest management practices which are ecologically sustainable in that they ensure the preservation of local winter bird diversity.

## Methods

### Study area

The study was carried out in winter 2004–2005 and 2005–2006 in deciduous forests (39,761 km<sup>2</sup>) in Asti province, north western Italy (Fig. 1). The area is hilly (110–330 m a.s.l.) and characterized by a sub-continental climate with Mediterranean influences. The commonest forest management system is coppice, which produces patches at different growth stages, often grown with scattered single-stem trees or standards (mostly 80–100 years old oaks), which are felled at longer intervals. Human activities have always had a severe impact on forests, which have been harvested since the 17th century (Correggia 2002). 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 year-old black locusts (73.71% of forest cover), oaks *Quercus petraea*, *Q. pubescens*, *Q. cerris* and *Q. robur* (14 of 47% cover), sweet chestnuts *Castanea sativa* and poplars *Populus* ssp. (mostly in plantations). Oaks occur both as scattered standards in black locust woodlots and as associations (*Phytospermo-Quercetum petraea*, *Polygonato multiflori-Quercetum roboris*, *Querco-carpinetum*). (Picco and Ravetti 2000).

### Bird counts

Birds were counted by 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, during the first 4 h after sunrise, from December to February 2004–2005 and 2005–2006. To maximize detections, the observer (EC) walked across the diameter of the circular plot at the end of a 10 min sampling period. 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; the largest values from the two censuses 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 each plot was established in the field by means of a global positioning system (GPS), Garmin eTrex<sup>®</sup> Navigator (Garmin Corporation, Olathe, KS).

Avian communities were described in terms of bird species richness (S), diversity (Shannon index  $H' = -\sum p_i \ln p_i$ , where  $p_i$  is the relative frequency of species  $i$ , (Shannon and Weaver 1949)) and abundance of individuals.

### Habitat structure

Habitat structure measurements were made between the first and the second census visit, with the vegetation plots centered in the avian census plot. At each point we described the vegetation structure by using the Bitterlich variable plot-radius method (Bitterlich 1948). The Bitterlich method provides an easy, fast and simple way of estimating tree abundance as basal area per hectare. With the use of an angle-gauge all trees that are larger in diameter than a specified angle are counted in a circle from a central sampling point. For each counted tree 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), understory density (the distance

between the closest shrubs was measured 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 ( $= \text{SD}/\text{mean} * 100$ ) of height and diameter measurements. We also estimated the number of trees per hectare (NT/ha) and using the national forest inventory double entry tables (Castellani et al. 1984) we computed the volume of biomass for each tree species present, from which the mean value of total volume (BV, in  $\text{m}^3$ ) and the relative volume percentage of each tree species (QB for oak, BLB for black locust and OB for volume of other trees) was derived. The percentage of ivy cover on the ground and on the trees and the volume of standing dead trunks was also subjectively assessed and recorded.

### Landscape pattern

Land-use classification was based on updated regional forest plan maps (1:10.000) (IPLA—Regione Piemonte 2005a, b). Due to the focus on forest birds, only landscape configuration variables related to forests were assessed; non-forest habitat types were considered as background. We converted our maps to rasters, with 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 (McGarigal et al. 2002) was used to calculate landscape variables (or metrics). Nine class-level metrics and nine landscape-level metrics (in Fragstats' terminology) were considered (Table 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 refer to the above metrics by using italics. Class-level metrics were calculated for each habitat type, resulting in twenty-seven measurements (9 metrics per 3 habitat types). We derived all landscape- and class-level metrics by generating circular buffers with a radius of 1,000 m around each sampling plot using ArcGis 9.1 (Esri 2004). We estimated that a 1,000 m radius was representative of the diversity of habitats available to forest birds, due to the high winter mobility of most birds species populating our study area. The Modifiable Areal Unit Problem (MAUP) can cause spurious results in GIS-based landscape analyses (Jelinski and Wu 1996), since these analyses are sensitive to extent and grain size (Wu 2004). We avoided such problems by using the same extent and grain size for all sites, and by using 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 the sites, minimizing problems unique to each index (Li and Wu 2004). Sites were categorized into habitat types that were relevant to both management and our study species.

### Data analysis

#### Bird community

Spatial autocorrelation among plots was tested by comparing residuals of bird community models by using the Moran's index (*I*) as a function of spatial distance (Legendre and Legendre 1998; Sawada 1999) This index indicates the degree of similarity/dissimilarity between the values of the variable considered and ranges approximately from +1 (aggregated distribution) to -1 (regular distribution). Values of *I* are approximately equal to zero when arrangement is random, specifying 26 lag intervals up to a maximum distance of 30 km. Correlograms plot the Moran's *I* coefficients

against distances between localities (Legendre and Fortin 1989). Absence of spatial autocorrelation can be identified when the line is close to zero (i.e., sampling data are spatially independent). To test the significance of these Moran's coefficients for each lag distance, 999 Monte Carlo permutations of the original data were performed and its P-values were calculated (Sawada 1999 and Heikkinen et al. 2004). The Moran's correlogram as a whole is considered significant if at least one of its coefficients is significant at the probability level after progressive Bonferroni correction ( $P \leq 0.01$ ). Moran's I statistics and correlogram were computed using the program ROOKCASE (Sawada 1999). Since we found no spatial autocorrelation of residuals of the models we did not take into account any spatial autocovariate in the models.

Structural habitat variables are intrinsically correlated. Hence, much of the information in one or more of these variables can be redundant and the results of analyses based on these raw predictors may be ambiguous (Jongman et al. 1995). Principal Component Analysis (PCA: Gauch 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 in an SPSS package for Windows (SPSS Inc 2003).

Many landscape metrics calculated with Fragstats were also correlated. In this case, given that PCA generated ambiguous derived components, we performed different variable reduction procedures before proceeding to the statistical modeling phase. In order to avoid multicollinearity among variables we first examined all pairwise correlations to identify correlated pairs ( $r > |0.7|$ ). Following Ritters et al. (1995), one variable was selected to represent each group of highly correlated variables and selection criteria included the degree of normality and our subjective estimate of interpretability. This procedure reduced the number of class variables from 27 to 10 and that of landscape variables from 9 to 6.

We used generalized linear models (GLM) to test for the effects of habitat variables (three scores of PCA, percentage of ivy at ground, percentage of ivy on trees, oak volume percentage, black locust volume percentage, volume of other trees percentage) and of landscape variables (see Table 1) on bird community parameters (i.e. bird species richness, diversity and abundance).

Finally, we tested all pairwise correlations to identify correlated pairs of significant habitat, class- and landscape-level variables ( $r > |0.7|$ ) and since these variables were not correlated we merged them to carry out GLMs with a backward stepwise procedure to point out the most important habitat and/or landscape predictors. Landscape and habitat variables were log-transformed [ $y = \log(x + 1)$ ] to attain normal distributions before running GLMs. 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. Generalized linear models and AIC were calculated using the R package (Ihaka and Gentleman 1996; R Development Core Team 2005).

## Results

Overall, 2404 individuals representing 32 species were sampled in 200 plots (see Supplementary material for a complete list of bird species and frequencies of occurrence). Robin *Erithacus rubecola*

and Great Tit *Parus major* were the commonest species, with frequencies of occurrence higher than 60%. Blackbird *Turdus merula*, Blue Tit *Cyanistes caeruleus*, Marsh Tit *Poecile palustris*, Wren *Troglodytes troglodytes* and Chaffinch *Fringilla coelebs*, were also rather common, with frequencies between 40 and 50%, followed by Great Spotted Woodpecker *Dendrocopos major*, Jay *Garrulus glandarius* and Nuthatch *Sitta europaea* (frequencies of occurrence between 30 and 40%).

#### Bird community–habitat relationships

The first three principal components (PC1, PC2, PC3) accounted for 79.96% of total variance in the habitat structure matrix, with eigenvalues >1 (Table 2). 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 younger to older stands. The coefficient of variation of tree height and diameter provided major positive loadings on PC2, and shrub density showed a positive correlation with PC3 (Table 2).

The results of generalized linear models of bird species richness, diversity and abundance in relation to habitat structure are shown in Table 3. All variables considered were best modeled by combinations that included the percentage of oak biomass. Abundance of individuals and bird species richness were modeled by PC1 (suggesting that the numbers of species and individuals were higher in older woods) and abundance of individuals was also negatively correlated with the percentage of black locust biomass.

#### Bird community–landscape relationships

The results of generalized linear models of bird community parameters are shown in Table 4.

At the class-level, all bird community parameters were best modeled by combinations of variables that included the oak core area, which was positively correlated with community parameters.

At the landscape-level, bird species diversity was negatively correlated with LAND\_ENN; abundance of individuals was positively correlated with LAND\_TE and LAND\_CORE and negatively with LAND\_PARA, LAND\_ENN and LAND\_MESH. Bird species richness was positively associated with LAND\_TE and LAND\_CORE and negatively correlated with LAND\_ENN.

#### Bird community–habitat plus landscape relationships

Table 5 presents the results of generalized linear models of bird community parameters in relation to habitat and landscape (both class- and landscape-levels) predictors that significantly affected previous models (i.e. those minimizing AIC).

The best predictor was oak core area, which was positively correlated with all community parameters. Oak biomass and PC1 (two habitat predictors) were positively correlated with bird species diversity and richness, while abundance of individuals was only influenced by PC1; no landscape variables entered the species diversity model, LAND\_PARA and LAND\_ENN were



negatively correlated with abundance of individuals and species richness was negatively correlated with LAND\_ENN.

## Discussion

Forest management can promote dramatic changes in vegetation characteristics (Palik and Engstrom 1999) which, in turn, may affect habitat and landscape structure. In our study area, human pressure has led to severe cutting of native forests to make room for agriculture, with a subsequent loss and fragmentation of forest habitat. In addition, forestry practices favored black locust (73.71% of forest cover), an alien species which has established itself at the expense of native oaks. Changes in habitat structure 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 (Thompson et al. 1999; Laiolo et al. 2003).

Our results showed that at the habitat level, species diversity, abundance of individuals and species richness were higher in mature stands with high values of oak biomass. In winter, stand age is assumed to be an important predictor of bird community parameters, but the presence of oaks in these stands is what makes the difference, since old oak stands still yield sufficient amounts of both plant (acorns) and animal (invertebrates living in decaying wood) food for birds (Ferry and Frochot 1990). Moreover, because of their greater volume, mature trees sustain large populations of phytophagous insects (Lack and Lack 1951; Moss 1978; Helle and Mönkkönen 1990). Black locusts likely supports less insect food because of their smaller volume and/or because a rich invertebrate fauna specialized to feed on its wood has not yet evolved (Laiolo et al. 2003). Present-day Italian selective cutting practices allow black locust woods to be regularly harvested on condition that some oak stems are retained. Although this practice prevents the evolution of a natural succession and the achievement of fully mature forests, it helpfully mitigates the local reduction of native oaks.

Generalized Linear Models showed that, at the class-level, all bird community parameters were best modeled by a combination of variables that included oak core area. This means that bird species richness, diversity and abundance are positively affected by their proximity to large forests dominated by native oaks.

At the landscape-level, the sum of perimeters of all patches (LAND\_TE) was positively correlated with the abundance of individuals. It should be noted that LAND\_TE measures edges between forest patches; hence the increase in total edges mostly depends, in our case, on the increase in adjacent, contiguous patches with different forest management. This suggests that forestry diversification of patches per se, may be sustainable. LAND\_MESH was negatively correlated with bird species richness and abundance of individuals. This metric denotes the size of the areas when the region under investigation is divided into different areas and characterizes the fragmentation of a region independently of its size (Jaeger 2000). The negative correlation suggests that the increasing fragmentation at the landscape-level significantly affects forest bird communities, as already shown for prairie communities (Koper and Schmiegelow 2006).

Perimeter-area ratio (LAND\_PARA) was negatively correlated with the abundance of individuals and species richness. This indicates that the shape of patches may significantly affect bird communities and that, area being equal, bird abundance and diversity parameters are lower in narrow forest strips than in compact patches (Tubelis et al. 2007). Some community parameters were also negatively associated with LAND\_ENN, a connectivity measure of the distance between patches. This confirms that forest fragmentation plays a negative role for bird communities (Paton 1994; Enoksson et al. 1995; Chalfoun et al. 2002; Batáry and Báldi 2004).

Although some studies have simultaneously addressed the influence of habitat and landscape on bird communities (Telleria and Santos 1995; Jokimäki and Huhta 1996; Perkins et al. 2000; Brotons

and Herrando 2001; Brotons et al. 2004; Telleria et al. 2001), few studies have looked contextually at habitat structure and landscape and the question of how wintering birds respond to environmental factors has not been fully answered (Shochat and Tsurim 2004).

When we analyzed the effects of habitat, class- and landscape-level metrics together, GLMs showed that the local bird community was controlled by habitat and class-level metrics related to the presence of native oaks (i.e. oak biomass percentage and oak core area). Bird species richness, diversity and abundance were in fact best modeled by a combination of factors including at least one oak-related predictor describing the habitat or landscape (class-level) composition. Landscape-level metrics that entered the models indicate negative effects due to the lack of connectivity and the shape of the forest patches, showing that even very coarse parameters of landscape structure indicate what is important for forest birds (Bailey et al. 2007).

The poor bird attractiveness of the black locust (demonstrated both by habitat and landscape analyses) may be a threat to local bird communities because the black locust matrix may lower the connectivity of the forested landscape. It is interesting to notice that, at the landscape-level, total forest area (LAND\_AREA) is never significant; this may indirectly confirm that large black locust-dominated forested areas have no significant effects on bird communities. Hence, our study, while confirming that forest integrity is indispensable to preserve species richness (Telleria and Santos 1995; Doherty and Grubb 2000; Turcotte and Desrochers 2005), also suggests that integrity should be obtained through the maintenance of native tree species (Tubelis et al. 2007).

The present multi-level approach (habitat, class- and landscape-level analyses) made it possible to delineate patterns of co-variation between community parameters and habitat and class-level oak-related predictors. Our findings clearly show that the retention of native oaks both at the habitat and landscape scale is the key-factor for the conservation of winter bird diversity in the deciduous woods of our study area. Protecting biodiversity in fragmented landscapes requires substantial conservation and ecosystem restoration efforts (Young 2000; Lindenmayer et al. 2003). 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, so that they may serve as ‘stepping stones’, contributing to landscape connectivity and thus ensuring movements and foraging resources through the entire landscape (Fischer and Lindenmayer 2002). To face bird community requirements at the landscape scale, we must ensure the maintenance of large oak patches, possibly in close proximity in order to avoid severe fragmentation effects. Long term management should aim to reinstate a more natural forest composition, favoring the spread of oaks and other native trees, since the spread of alien species may be detrimental for biodiversity (Tubelis et al. 2007). If cut, black locusts sprout quickly from roots and stumps and grow faster than other tree species, thus becoming dominant. However, strategies for influencing land-use need to consider the demand for fuel-wood (Gruenewald et al. 2007), and any action to preserve habitat must take into account the conflicting interests of the private owners of woodlots. This could be achieved by allowing selective cutting of small black locust woodlots, controlling the spread of black locusts, favoring the establishment of native vegetation after logging and limiting the removal of understory vegetation and dead trunks. These very simple actions, with minimal habitat alterations, may help achieve forestry management practices that protect typical forest bird species and possibly increase species diversity.

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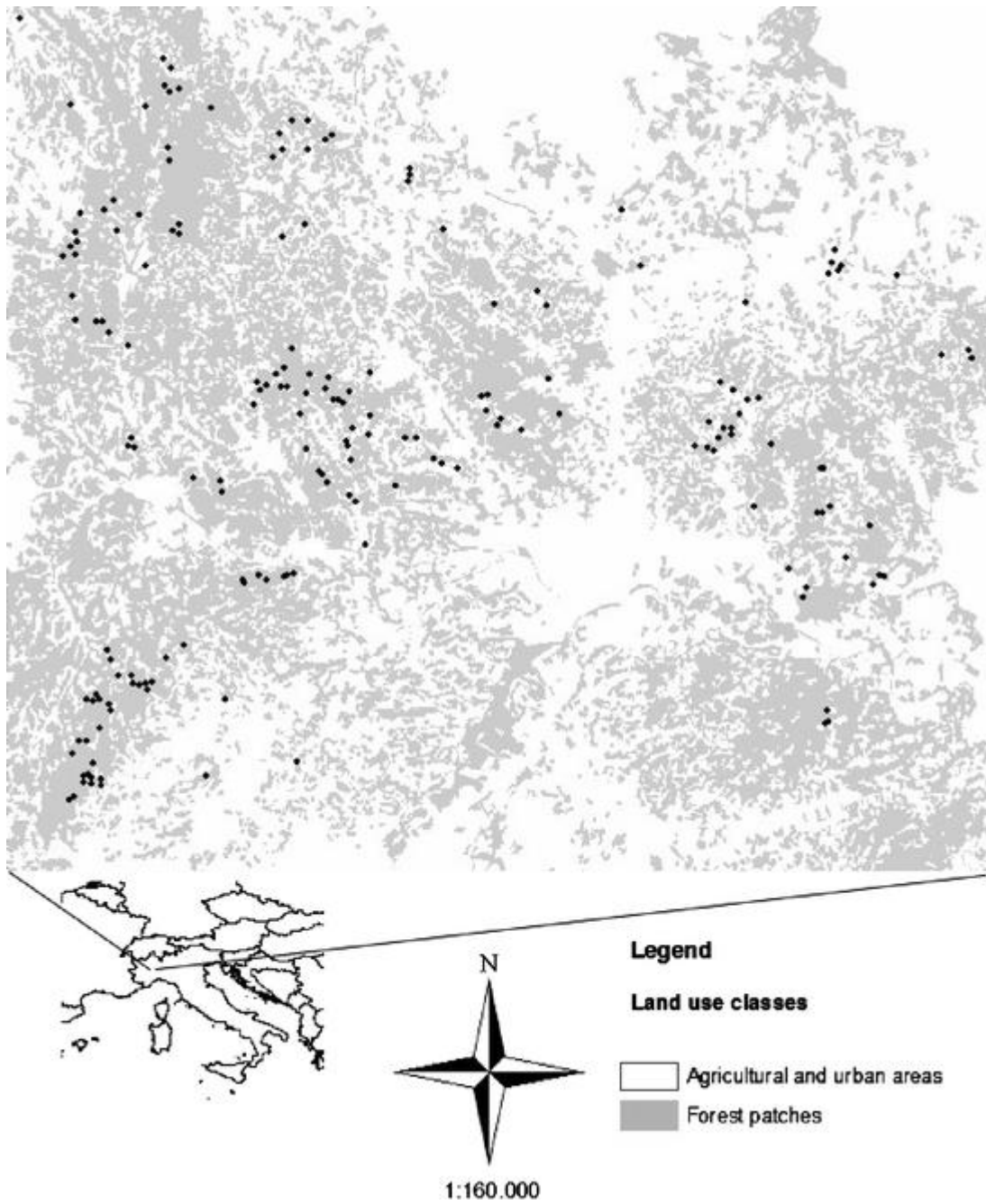


Fig. 1  
Geographical location of plots and map of the study area (black dots). Forest area (light grey) and agricultural and urban areas (white) are shown

Table 1

Land-use metrics derived through FRAGSTATS describing forest fragmentation at class and landscape <sup>a</sup> level

	<b>Description</b>
<b>Class level variables<sup>b</sup></b>	
CA	Class area (ha)
NP	Number of class patches
TE	Sum of perimeter of class patches (m)
SHAPE	Average of total length of patch edge to the minimum possible perimeter for maximally compact patch ratios, computed for same class type
PARA	Ratio of the patch perimeter (m) to area (m <sup>2</sup> )
CORE <sup>d</sup>	Average of areas (m <sup>2</sup> ) within the patches that are farther than the specified depth-of-edge distance from the patch perimeter divided by 10,000 (ha)
PROX	Average of all patches within the buffer, of the ratio of patch area (m <sup>2</sup> ) to nearest neighbor edge-to-edge distance (m)
ENN	Average of Euclidean Nearest Neighbour distance
MESH	Sum of all same class patches area squared, divided by the total landscape area (m <sup>2</sup> ), divided by 10,000 (ha)
<b>Landscape level variables<sup>c</sup></b>	
LAND_AREA	Forest area (ha)
LAND_NP	Number of patches
LAND_TE	Sum of perimeters of all patches (m)
LAND_SHAPE	Average of total length of patch edge to the minimum possible perimeter for maximally compact patch ratios, computed for all patches
LAND_PARA	Ratio of the patch perimeter (m) to area (m <sup>2</sup> )
LAND_CORE <sup>d</sup>	Average of areas (m <sup>2</sup> ) within the patches that are farther than the specified depth-of-edge distance from the patch perimeter divided by 10,000 (ha)
LAND_PROX	Sum of patch area (m <sup>2</sup> ) divided by the nearest edge-to-edge distance squared (m <sup>2</sup> ) between the patch and the focal patch of all forest patches whose edges are within a specified distance (m) of the focal patch
LAND_ENN	Average of Euclidean Nearest Neighbour distance
LAND_MESH	Sum of all patches area squared, divided by the total landscape area (m <sup>2</sup> ), divided by 10,000 (ha)

<sup>a</sup>Variable descriptions from McGarigal et al. (2002)

<sup>b</sup>Includes only the specified focal habitat type within the landscape. Calculated for the following habitat types: oak forest, black locust forest, other forests

<sup>c</sup>Includes all habitat types within 1,000 m radius surrounding each sampling point

<sup>d</sup>Edge depth was set at 50 m for birds based on the range of edge effects for different taxa presented in Paton (1994)

Table 2

Results of PCA carried out on eight habitat structure variables

<b>Variables</b>	<b>Factor loadings</b>		
	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>
Number of trees per hectare (NT/ha)	<b>-.707</b>	.303	.106
Total biomass volume (m <sup>3</sup> ) (BV)	<b>.717</b>	-.083	.027



Shrub density (SD)	.040	.001	.993
Mean tree height (m) (TH)	<b>.942</b>	-.099	-.029
Coefficient of variation of tree height (%) (CVH)	.061	<b>.897</b>	<b>-.093</b>
Mean tree diameter (cm) (DBH)	<b>.929</b>	.133	-.015
Coefficient of variation of tree diameter (%) (CVD)	.179	<b>.894</b>	.056
Canopy height (m) (CH)	<b>.923</b>	.032	.056
Percentage variance explained	45.66	21.62	12.68

The highest factor loadings are in bold type

Table 3

Generalized linear models of bird species diversity, abundance and species richness, in relation to habitat structure predictors [PCA scores for habitat structure variables (see Table 2), percentage of oak volume, percentage of black locust volume, basal area, percentage of ivy cover on ground and on trees]

**Habitat**

<b>Predictor</b>	<b>Beta</b>	<b>SE</b>	<b>P</b>
Species diversity			
Oak volume percentage	0.175	0.038	<0.001
AIC: 185.19			
Abundance			
Oak volume percentage	0.109	0.042	<0.01
Black locust volume percentage	-0.076	0.040	<0.05
PC1	0.055	0.030	<0.05
AIC: 1192.9			
Species richness			
Oak volume percentage	0.112	0.047	<0.01
PC1	0.069	0.041	<0.05
AIC: 782.95			

Only models with lower AIC are shown

Table 4

Generalized linear models of bird species diversity, abundance and species richness, in relation to class- and landscape-level (Table 1)

<b>Class-level</b>				<b>Landscape-level</b>			
<b>Predictor</b>	<b>Beta</b>	<b>SE</b>	<b>P</b>	<b>Predictor</b>	<b>Beta</b>	<b>SE</b>	<b>P</b>

Species diversity							
Black locust ENN	-0.3737	0.1447	<0.05	LAND_ENN	-0.4261	0.0648	<0.05
Oak core area (CORE)	0.5969	0.2317	<0.05				
AIC = 181.43				AIC = 197.72			
Abundance							
Black locust ENN	-0.5935	0.1178	<0.001	LAND_TE	1.1559	0.3660	<0.01
Oak core area (CORE)	0.7067	0.1313	<0.001	LAND_PARA	-0.4747	0.2097	<0.05
Oak ENN	-0.1841	0.0793	<0.05	LAND_CORE	0.7053	0.2403	<0.01
AIC = 1178.4				LAND_ENN	-0.5912	0.1471	<0.001
				LAND_MESH	-0.2531	0.1216	<0.05
				AIC = 1192			
Species richness							
Oak core area (CORE)	0.6912	0.1656	<0.001	LAND_TE	0.5366	0.3639	<0.05
AIC = 787.31				LAND_CORE	0.2681	0.1299	<0.05
				LAND_ENN	-0.3941	0.1956	<0.05
				AIC = 791.62			

Only models with lower AIC are shown

Table 5

Generalized linear models of bird species diversity, abundance and species richness, in relation to best predictors of habitat structure, class and landscape (Table 1)

**Habitat, class- and landscape-levels**

Predictor	Beta	SE	P
Species diversity			
Oak volume percentage	0.1262	0.0390	<0.01
Black locust ENN	-0.2995	0.1411	<0.05
Oak core area (CORE)	0.6932	0.1993	<0.001
AIC: 173.82			
Abundance			
PC1	0.1042	0.0290	<0.001
Black locust ENN	-0.4919	0.1283	<0.001
Oak core area (CORE)	0.6196	0.1323	<0.001
LAND_PARA	-0.6560	0.1997	<0.01
LAND_ENN	-0.3958	0.1460	<0.01
AIC: 1135.8			
Species richness			
Oak volume percentage	0.2322	0.1033	<0.01
PC1	0.1260	0.0326	<0.001
Oak core area (CORE)	0.5317	0.1725	<0.01
LAND_ENN	-0.3761	0.1786	<0.05
AIC: 770.82			

Only models with lower AIC are shown