



How does forest species specialization affect the application of the island biogeography theory in fragmented landscapes?

Olivia Dondina, Valerio Orioli, Pamela D'Occhio, Massimiliano Luppi and Luciano Bani*

Department of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza 1, I-20126 Milano, Italy

ABSTRACT

Aim Overall species richness in habitat remnants is seldom explained by the island biogeography theory (IBT). In this study, we tested the effectiveness of the IBT in explaining species richness of forest birds with or without considering the effect of the different forest specialization of species (*generalist*, *edge* and *interior*; community analysis). We also identified single species and groups of species that could serve as indicators of different fragmentation degrees (indicator species analysis).

Location Broadleaved forests in western Lombardy (northern Italy).

Methods We evaluated bird species richness in 344 forest fragments. Fragment area (FA), distance from the nearest source area (> 1000 ha) (DSA) and number of neighbouring fragments (NF) were calculated for each fragment. Using Poisson generalized linear models, we compared a model that evaluated the relationships between fragment covariates and species richness to a model that also considered the effect of forest species specialization on each relationship. Moreover, we investigated the association between each species and particular fragmentation conditions by calculating the IndVal index.

Results The application of the IBT to species richness performed significantly better if we took into account forest species specialization when evaluating the effect of fragment covariates. In particular, the positive effects of FA and NF and the negative effect of DSA were significantly stronger on *interior* species rather than on *generalist* and *edge* species. Using the IndVal index we identified six species in three groups strongly associated with specific fragmentation degrees.

Main conclusions The results showed the strong influence of the specialization of species on their distribution in fragmented landscapes. *Interior* species were the best candidates as a proxy of fragmentation effects. However, the indicator species analyses revealed that not all *interior* species showed the same sensitivity to fragment covariates.

Keywords

archipelago effect, bird communities, broadleaved forest ecosystems, distance effect, habitat remnants, indicator species, IndVal, interior species, Lombardy, species–area relationship

*Correspondence: Luciano Bani, Department of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza 1, I-20126 Milano, Italy.
E-mail: luciano.bani@unimib.it

INTRODUCTION

Habitat destruction, alteration and fragmentation are recognized as the most serious threats to global biodiversity because they are the human-induced phenomena with the

strongest effects on animal species distribution (Debinski & Holt, 2000; Fischer & Lindenmayer, 2007). Two theories describe the species ecology within habitat remnants: the island biogeography theory (IBT; MacArthur & Wilson, 1967) and the metapopulations theory (Levins, 1969; Hanski,

1998). The first theory describes the effects of habitat fragment size and isolation on species richness (Debinski & Holt, 2000): the smaller and more isolated the fragments are, the fewer species are expected to occur within them (Diamond, 1975; Wilson & Willis, 1975; Terborgh, 1976). The second theory describes the spatial arrangement and dynamics of subpopulations in fragmented landscapes (Arnold *et al.*, 1993; Hanski & Gilpin, 1997; McCullough, 1997; Hanski & Gaggiotti, 2004). Several studies combined these two theories to explain species richness as the balance between extinction and colonization in fragmented terrestrial contexts. According to the IBT and the metapopulations theory, these processes depend on the physical characteristics of residual habitat fragments, such as their size and distance from source areas (e.g. large blocks of habitat), and the surrounding landscape context (e.g. the number of neighbouring habitat fragments) (Collinge, 1995; Laurance & Bierregaard, 1996; Lindenmayer *et al.*, 2002; Watson *et al.*, 2004). However, in some cases the results of these studies were different from the expected results (Margules, 1996; Schemielgelow *et al.*, 1997; Davies & Margules, 1998). Indeed, several mechanisms could confound the simple relationships on which IBT predictions are based (Triantis & Bhagwat, 2011). Among these, recent studies highlighted the role of species-specific life history traits in affecting colonization–extinction processes (Öckinger *et al.*, 2010; Franzén *et al.*, 2012). In particular, in terrestrial contexts the relationships between species richness and fragment area (FA) and isolation, as postulated by the IBT, are often masked by the lack of an abrupt contrast between suitable and unsuitable habitats (as in the case of an island surrounded by an ocean) and by the absence of a highly impermeable matrix (as the ocean is for terrestrial island species). Indeed, species richness in habitat fragments in these contexts is determined by the presence of species with different forest specializations, such as species intimately linked to habitat remnants (interior species), species linked to habitat remnants but not so negatively affected by the adjacent matrix (generalist species), or species that require the presence of transitional habitats (edge species). The IBT was actually developed for oceanic islands, where communities are typically closed or unitary (*sensu* Clements, 1916), and may be viewed as units operating mainly within themselves, whereas in terrestrial contexts communities are typically open (*sensu* Gleason, 1926). Additionally, results different from those postulated by the IBT can occur in terrestrial landscapes because species-specific biological traits (e.g. dispersal capability and reproductive potential) lead to a strong differentiation in species immigration and extinction rates because of the high variability of both remnant quality and matrix permeability. Thus, the combination of different specializations and specific biological traits determine a high heterogeneity in species responses to fragmentation (see Betts *et al.*, 2014). On the one hand, the preference of some species for small fragments can mask the species–area relationship as postulated by the IBT (Matthews *et al.*, 2014). In particular, higher species richness in small fragments, where

the ratio of edge and core area is maximized, could be due to a high number of edge species (Paton, 1994) or to the prevalence of generalist species in the overall species richness (Gascon & Lovejoy, 1998). On the other hand, the negative effect of isolation on species richness could be masked by the species' biological traits (Watson *et al.*, 2004). For example, some species are not affected by isolation because they are highly mobile (Margules *et al.*, 1982; Ambuel & Temple, 1983) or because they are not so negatively affected by the matrices surrounding their habitat patches (Andrianarimisa *et al.*, 2000; Renjifo, 2001). Despite these caveats being widely known, there are still relatively few empirical studies that explicitly address how ecological and biological traits affect the relationship between species distribution and spatial covariates in fragmented landscapes (e.g. Henle *et al.*, 2004; Bommarco *et al.*, 2010; Matthews *et al.*, 2014). Clearly, this has a great importance from a conservation point of view when the intent is to use species, or groups of species, as surrogates of fragmentation degree.

This study was aimed at investigating how the forest species specialization can affect the application of the IBT on bird communities in fragmented broad-leaved forests within a wide area in northern Italy. First, we evaluated the robustness of the application of the IBT on the richness of *forest-dependent* species (i.e. excluding all matrix species). Subsequently, we evaluated the robustness of the application of this theory to three groups of species characterized by a different forest specialization: *generalist*, *edge* and *interior* species (community analysis). Finally, to identify indicator species for different degrees of fragmentation, we investigated the association of each species with specific combinations of IBT spatial covariates (indicator species analysis).

The community analysis will lead to the identification of groups of species with a specific specialization that responded better to IBT predictions and, thus, are more sensitive to forest fragmentation. In other words, we will be able to identify the groups that could be used as indicators of landscape fragmentation. However, the richness of groups of species with a specific specialization might not always be the most valuable proxy of fragmentation because it does not take into account species-specific biological traits. On the other hand, the indicator species analysis will allow us to identify single species, or groups of species, which could serve as indicators of specific fragmentation contexts. In particular, as highlighted from other studies (see Bani *et al.*, 2006), we expect that *interior* species will respond better to IBT predictions and that they will also be selected as indicators for different fragmentation contexts.

MATERIALS AND METHODS

Study area

The study was carried out in the western part of Lombardy (northern Italy) in an area of c. 9000 km² where forests cover 23% of the total surface. The study area can be divided

into three main subregions: the Prealps in the North, the lowland (below 300 m a.s.l.) in the central part, and the Apennines in the South (Fig. 1). The Prealps and the Apennines are characterized by a mainly continuous forest cover. The lowland is crossed from North to South by the Ticino Natural Park, a 220 km² wide protected area with residual continuous forests following the course of the Ticino River. The remaining part of the lowland area has been highly modified; intensive corn crops prevail in the central and eastern parts and rice paddies prevail in the West (Bani *et al.*, 2006). Small, residual broadleaved forest fragments (95% of which are smaller than 10 ha) are scattered in the lowland cultivated area.

Bird data

Bird data were obtained from a long-term monitoring programme of breeding birds in Lombardy (Bani *et al.*, 2009). This type of large-scale project has the advantage of providing a large amount of data collected over wide areas. However, studies performed on this type of data set involve dealing with a sampling design not specifically addressed to test the hypothesis formulated in the study. In addition, they usually do not include multiple surveys in the same season, which makes it impossible to account for species detection probability. In particular, the Lombardy breeding bird monitoring programme does not even rely on fixed sites because the sampling units are randomly extracted each year.

The variability of species-specific detection probability is a potential problem in studies aimed at estimating species richness. Therefore, the use of multi-species data requires the assumption that detection probability does not have a strong effect on inferences (Morelli, 2015). In our opinion, the large data set used for this research may limit this potential bias, at least by reducing the noise produced by stochasticity in the detection of the rarest species.

Data were collected using a standardized method based on the unlimited distance point count technique (Blondel *et al.*, 1981; Fornasari *et al.*, 1998) with a minimum distance of at least 500 m between sampling locations. To limit the effects of the within-species detection probability, bird surveys were performed each year during the breeding season (10th May–20th June), from sunrise to 11.00 AM and only in good weather conditions (sunny to cloudy, without rain or strong winds). The point count technique allows detection of bird species pertaining to *Columbiformes*, *Cuculiformes*, *Apodiformes*, *Coraciiformes*, *Piciformes*, *Passeriformes*, as well as common raptors (Bani *et al.*, 2009).

For this research, we selected all the point counts undertaken in forest patches or within a 250 m buffer around them. We chose this distance because it could be considered the maximum detection distance for most of the bird species surveyed. We only selected point counts performed from 2007 to 2014 because no significant changes in broadleaved forest cover (< 0.3%) occurred during that period in the study area. This was verified by comparing the available DUSAF 1:10,000 digital maps [Destinazione d'Uso dei Suoli Agricoli e Forestali (Classification of Agricultural and Forest Lands)]: DUSAF 2.1 (ERSAF, 2007) and DUSAF 4 (ERSAF, 2014). To evaluate the effect of forest fragmentation, we only considered *forest-dependent* species, defined as those species breeding in forest habitats. In addition, we only considered the species that were evenly distributed throughout the study area to ensure that occasional species associated with localized habitat types would not affect within-fragment species richness. Subsequently, we divided the whole set of *forest-dependent* species into three specialization groups, based on literature information. We adopted the classification proposed by Bani *et al.* (2006), who classified the bird species according to differences in their abundance in forest cores and edges, revised following Cramp & Simmons (2006). Thus, forest birds were classified as *generalist*

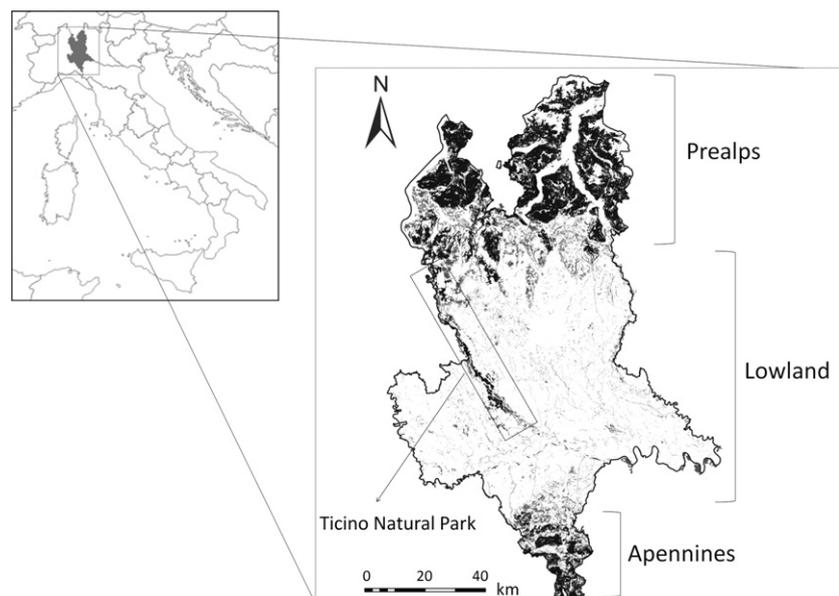


Figure 1 On the left is the location of the study area in northern Italy. On the right is the study area with broadleaved forest cover in the background. Forest source areas (i.e. patches larger than 1000 ha) are in black; forest fragments are in grey.

(forest-dependent species inhabiting either edge or interior habitats), *edge* or *interior* species (see Appendix S1 in Supporting Information).

Landscape data

For land use cartography, we used the most recent digital map available for the study area (DUSAF 4; ERSAF 2014). In particular, we took into account all patches belonging to one of the following categories of forest cover: broadleaved forests (DUSAF class: 311), mixed forests (DUSAF class: 313) and broadleaved reforestations (DUSAF class: 314). Using ARCGIS 10 (ESRI, 2011), we merged all fragments that were < 25 m apart. We chose this threshold because it represents the width of a typical secondary road, the digitization of which often leads to a subdivision of a single forest patch (as would be perceived by birds) in different forest polygons. To avoid the sample size effect for large fragments (larger than 100 ha), which could affect the characterization of bird communities, we only selected forest patches with a point count density higher than 1 point/100 ha. We considered a total of 366 patches. As we were interested in ascertaining the effects of forest fragmentation, we also excluded all patches larger than 1000 ha, which could be considered as source areas (Watson *et al.*, 2004). In those large patches, the percentage of *forest-dependent* species detected ranged from 61% (for the smaller patch, just over 1000 ha) to 96% (for the larger patch, c. 575,000 ha) of the whole pool of *forest-dependent* species. For each of the 344 remaining forest fragments, we calculated the following three spatial variables: FA, minimum distance from the nearest source area (DSA), and number of neighbouring fragments in a buffer of 1000 m (NF). We considered the latter variable to account for the possible 'internal colonization' played by immigrants within the archipelago (Simberloff & Abele, 1982; Gotelli, 2008).

Community analysis

In the community analysis, we considered the maximum numbers of bird species detected during the sampling period in each fragment as statistical units split into the three specialization groups (*generalist*, *edge* and *interior*). By doing so, we were producing pseudo-replications; therefore, we ran a generalized linear mixed model (GLMM) with the fragment ID as a random effect (Triantis *et al.*, 2015). However, because this random effect did not explain any percentage of the variance of the dependent variable, we ran the models again applying a generalized linear model (GLM) without accounting for any random effect.

We compared the performance of two models with and without interaction between species specialization and the fragment covariates to evaluate how species specialization affects the robustness of the application of the IBT on bird species richness.

First, we performed a generalized linear model (GLM) using a Poisson distribution and species richness as the

dependent variable. Model covariates, as main factors, were the logarithm of FA, the logarithm of DSA, NF and the three-level factor of species specialization. To take into account the possible effect of forest management practices on species richness (see Dondina *et al.*, 2015), we included a two-level independent categorical variable in the models: coppices or high forests. This information was collected in the field during bird surveys and refers to the prevailing forest condition resulting from the management practice in each fragment. We checked for over-dispersion (Cameron & Trivedi, 1990) using the *AER* package in R (Kleiber & Zeileis, 2008). Moreover, because one of the most important assumptions of multiple regression analyses (such as GLMs) is that predictors should not be strongly correlated with each other (Zuur *et al.*, 2009), we checked for variable collinearity by means of the variance inflation factor (VIF) using the *usdm* package in R (Naimi, 2015), taking 3 as the maximum threshold (Zuur *et al.*, 2009). We also verified that all other GLM requirements were met by checking diagnostic plots. Moreover, because the Moran's *I* index (Moran, 1950) revealed spatial autocorrelation in the model residuals, we added the spatial coordinates of the centroid of each fragment to the model as covariates. By doing so, we removed the spatial autocorrelation of the residuals, as confirmed by the Moran Test. All the continuous independent variables were standardized.

We then ran a second model that also took into account the interactions between the three-level factor of species specialization and FA, DSA and NF (Matthews *et al.*, 2014; Triantis *et al.*, 2015).

To compare the two models, we evaluated their goodness-of-fit using the percentage of explained deviance, and we compared their explanatory power by the likelihood ratio test.

All the analyses were performed using R 3.1 (R Development Core Team, 2014).

Indicator species analysis

To identify species, or groups of species, that could play the role of indicators of specific fragmentation contexts, we investigated if any species were significantly associated with particular combinations of fragment spatial covariates. To achieve this aim, we used the indicator species analysis approach (Duf rene & Legendre, 1997; De Caceres & Legendre, 2009), which allowed us to determine species, or groups of species, associated with a prior partition of sites by calculating an indicator value (IndVal) index. The IndVal index is the product between specificity or positive predictive value (A), the probability that a surveyed site belongs to the group of sites where the target species is found, and fidelity (B), the probability of finding a target species in sites belonging to a particular group of sites. We then identified the highest association value between species and groups of sites using the IndVal index and we tested the statistical significance of this relationship with a permutation test (999 permutations).

Subsequently, we corrected for the occurrence of false positives using the multiple testing correction proposed by Benjamini & Hochberg (1995). We used the method proposed by De Caceres *et al.* (2010), an extension of the original IndVal index, to look for indicator species of either individual groups of sites or a combination of groups of sites. We used forest fragments as sites in our analysis and we partitioned them in clusters according to their FA, DSA and NF values, as well as according to forest management practice. For this purpose, we categorized each continuous spatial covariate into two classes, arbitrarily but sensibly chosen. We classified forest fragments into small (S; ≤ 2 ha) or large (L) according to FA, near (N; ≤ 5 km) or far (F) according to DSA, and with few (F; ≤ 5) or many (M) neighbouring fragments according to NF. We obtained 16 clusters by combining the two levels of the four variables (the three spatial covariates and forest management practice). To avoid a strong sample size effect, we considered only the 11 clusters with at least five sampling units. The Indicator Species Analysis was performed applying the *multipatt* function implemented in the *indicspecies* package ver. 1.7.1 in R (De Caceres & Legendre, 2009).

For each species significantly related to a cluster or a group of clusters, the analysis returns the square root of the IndVal index in addition to the values of the *specificity* (A) and *fidelity* (B). We then grouped all the species associated with the same cluster or group of clusters in the same IndVal group of species.

RESULTS

Bird survey

From 2007 to 2014, 1462 point counts were performed and 144 bird species were found, 40 of which were *forest-dependent* species linked to broadleaved or mixed forests, evenly distributed throughout the study area. The mean number of species detected at each point was $11.2 (\pm 0.096 \text{ SE})$, $8.7 (\pm 0.062 \text{ SE})$ of which were forest-dependent. We split the entire set of *forest-dependent* species into three ecological groups: *generalist* (19 species), *edge* (14 species) and *interior* (7 species). The mean number of species detected at each point was $5.7 (\pm 0.043 \text{ SE})$ for *generalist* species, $2.2 (\pm 0.03 \text{ SE})$ for *edge* species and $0.8 (\pm 0.022 \text{ SE})$ for *interior* species.

Community analysis

The GLM performed without taking into account the effect of species specialization on FA, DSA and NF accounted for 66% of the variance (Table 1). Both the logarithm of FA and NF had a significant positive influence on *forest-dependent* species richness. Conversely, the logarithm of the DSA showed a significant negative effect. The model also showed that *forest-dependent* species richness was on average higher in high forests than in coppices.

Table 1 Results of the Poisson GLM performed without taking into account the interaction between the three-level species specialization factor (*generalist*, *edge* and *interior*) and fragment area (FA), distance from the nearest source area (DSA) and number of neighbouring fragments (NF) in explaining the bird species richness observed in 344 forest fragments in the Lombardy administrative region in northern Italy. Forest management: two-level factor (high forest and coppice). East and North: coordinates of each fragment centroid. Species specialization: three-level factor (*generalist*, *edge* and *interior*). All the continuous independent variables were standardized. Forest management (coppice) and *Generalist* do not appear in the table because they represent the control levels of the forest management and species specialization factors, respectively. SE: standard error of estimates. *z*: Wald statistic for testing the hypothesis that the corresponding estimate is equal to zero (null hypothesis). $\text{Pr}(> |z|)$: probability that the null hypothesis is true. The model explained 66% of the null deviance.

Predictors	Estimate	SE	<i>z</i>	$\text{Pr}(> z)$
(Intercept)	1.545	0.026	60.033	< 0.001
log (FA)	0.080	0.022	3.716	< 0.001
log (DSA)	-0.120	0.021	-5.231	< 0.001
NF	0.061	0.021	2.943	0.003
Forest management (high forest)	0.234	0.051	4.620	< 0.001
East	0.014	0.019	0.748	0.454
North	-0.115	0.020	-5.776	< 0.001
<i>Edge</i>	-0.394	0.038	-	< 0.001
<i>Interior</i>	-2.652	0.094	-	< 0.001

The GLM performed considering the interactions between the three-level specialization factor (*generalist*, *edge* and *interior*) and FA, DSA and NF explained 72% of the variance (Table 2). The likelihood ratio test confirmed that this model had a significantly higher explanatory power than the model that did not consider the interactions between species specialization traits and fragment covariates ($\chi^2 = 174.94$, d.f. = 6, $P < 0.001$). In particular, the results of this model showed that the positive area effect was significantly higher for *interior* species than for *generalist* and *edge* species (Fig. 2a). Moreover, the negative relationship between species richness and DSA was significantly steeper for *generalist* species than for *edge* species and was significantly steeper for *interior* species than for *generalist* species (Fig. 2b). Finally, the model revealed that the positive relationship between species richness and NF was significantly steeper for *interior* species than for *generalist* and *edge* species (Fig. 2c). The results of models with and without interaction were not over-dispersed; dispersion indices were 1.105 ($P = 0.111$) and 0.927 ($P = 0.818$), respectively. The VIF revealed no collinearity among all predictors in the two models.

Indicator species analysis

Ten of the 40 forest-dependent species considered in the indicator species analysis were found to be significantly associated with one or more clusters of fragments. Based on their association with one or more clusters (measured by the

Table 2 Results of the Poisson GLM performed taking into account the interaction between the three-level bird species specialization factor (*generalist*, *edge* and *interior*) and fragment area (FA), distance from the nearest source area (DSA) and number of neighbouring fragments (NF) in explaining the bird species richness observed in 344 forest fragments in the Lombardy administrative region in northern Italy. Forest management: two-level factor (high forest and coppice). East and North: coordinates of each fragment centroid. Species specialization: three-level factor (*generalist*, *edge* and *interior*). All the continuous independent variables were standardized. Forest management (coppice) and *Generalist* do not appear in the table because they represent the control levels of the forest management and species specialization factors, respectively. SE: standard error of estimates. z: Wald statistic for testing the hypothesis that the corresponding estimate is equal to zero (null hypothesis). $\Pr(>|z|)$: probability that the null hypothesis is true. The model explained 72% of the null deviance.

Predictors	Estimate	SE	z	$\Pr(> z)$
(Intercept)	1.535	0.026	58.825	< 0.001
log (FA)	0.083	0.028	2.984	0.002
log (DSA)	-0.187	0.026	-7.283	< 0.001
NF	0.062	0.027	2.321	0.020
Forest management (high forest)	0.231	0.051	4.536	< 0.001
East	0.013	0.019	0.669	0.503
North	-0.110	0.020	-5.492	< 0.001
Interior	-3.183	0.134	-23.668	< 0.001
<i>Edge</i>	-0.379	0.039	-9.781	< 0.001
log (FA) \times <i>Edge</i>	-0.048	0.043	-1.113	0.266
log (FA) \times <i>Interior</i>	0.265	0.110	2.411	0.016
log (DSA) \times <i>Edge</i>	0.287	0.040	7.099	< 0.001
log (DSA) \times <i>Interior</i>	-0.542	0.089	-6.064	< 0.001
NF \times <i>Edge</i>	-0.034	0.043	-0.807	0.420
NF \times <i>Interior</i>	0.248	0.089	2.774	0.005

IndVal index), we combined the species into seven IndVal groups (Table 3) (Fig. 3). Six of these groups were composed only of one species, and one group included four species. The specificity, or positive predictive value (A), ranged from 0.32 for the Common Redstart *Phoenicurus phoenicurus* (L., 1758) to 0.92 for the Nightingale *Luscinia megarhynchos* CL Brehm, 1831, whereas the fidelity value (B) ranged from 0.31 for the Short-toed Tree-creeper *Certhia brachydactyla* CL Brehm, 1820 to 0.80 for the Common Redstart. The square root of the IndVal index ranged from 0.50 for the European Nuthatch *Sitta europaea* L., 1758 and the Common Redstart to 0.80 for the Chaffinch *Fringilla coelebs* L., 1758. The number of clusters to which the species pertaining to the same IndVal group were associated varied from a minimum of one (groups 1 and 3) to a maximum of nine (group 7).

DISCUSSION

Community analyses

Even if the IBT still represents an important basis for the identification of conservation measures (Matthews *et al.*,

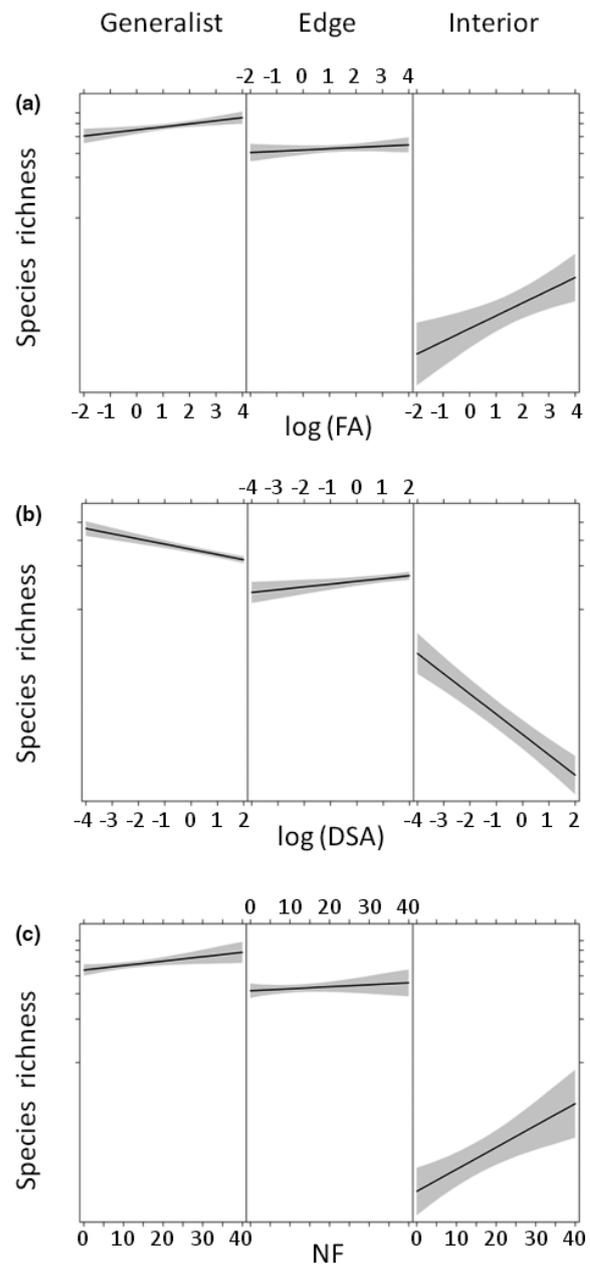


Figure 2 Relationships between bird species richness in Lombardy (northern Italy) and (a) fragment area (FA), (b) distance from the nearest source area (DSA), and (c) number of neighbouring fragments (NF) resulting from the GLM that took into account their interaction with species specialization (*generalist*, *edge* or *interior*). The black lines are the fitted values plotted on the linear predictor scale, whereas the y axis are labelled on the scale of the response variable (logarithm scale) to improve interpretation. The 95% confidence intervals of the fitted values are plotted in grey.

2014), its application in terrestrial contexts, for example, in forest fragmentation studies, is sometimes criticized (Mac Nally, 2007; Sekercioglu & Sodhi, 2007; Laurance, 2008) because some of the assumptions it requires are often not met (Watling & Donnelly, 2006). One of the most important violations results from the application of the IBT to the

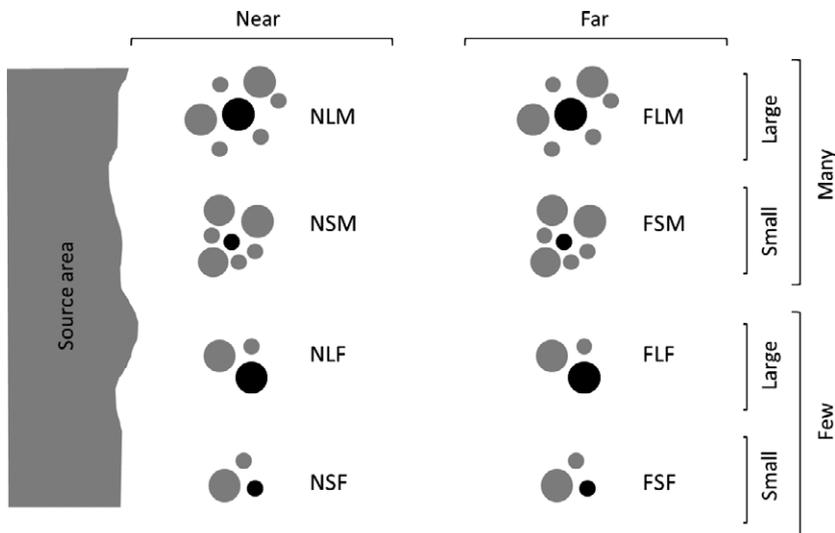


Figure 3 The eight clusters of forest fragments resulting from the combination of the three two-levels spatial covariates (distance from the nearest source area: DSA, Near [N] or Far [F]; fragment area: FA, Large [L] or Small [S]; number of neighbouring fragments: NF, Many [M] or Few [F]). On the left, in grey, is the source area; black dots are focal fragments to which spatial covariates are referred; grey dots are surrounding fragments.

overall species richness, which is typically comparable to an open community in terrestrial ecosystems. Some studies attempted to go beyond this limitation by splitting the overall species richness into homogeneous groups according to ecological or biological traits, more similar to closed communities (Henle *et al.*, 2004; Bommarco *et al.*, 2010; Öckinger *et al.*, 2010; Matthews *et al.*, 2014). In this study, we overcame the problem by splitting the overall species richness into the richness of three groups of forest species characterized by a different forest specialization (*generalist*, *edge* and *interior* species), and we compared the robustness of the application of the IBT to the overall richness of species with and without considering the effects of their specialization traits.

Our analysis revealed that the robustness of the application of the IBT to species richness is significantly higher if species specialization is taken into account when analysing the effect of each fragment covariate on species richness, rather than if only the effect of fragment covariates on species richness is considered. Indeed, the response of the overall species richness resulted from the combination of species with a different forest specialization, which could be characterized by opposite tendencies. In particular, the positive species–area relationship was found to be significantly higher for *interior* species than for *generalist* and *edge* species (Fig. 2a). Indeed, as suggested by several studies, the area effect is stronger for habitat specialists than for generalists (Brotons *et al.*, 2003; Krauss *et al.*, 2003; Magura *et al.*, 2008) because the first group can only inhabit fragments large enough to maintain a core area. Conversely, *edge* species richness was less affected by FA, probably because even small fragments, in which the perimeter/area ratio maximizes edge density [in our data set the mean perimeter/area ratio is 0.075 (SE: 0.002) in fragments smaller than 2 ha and 0.042 (SE: 0.001) in fragments larger than 2 ha], may prove suitable for these species (Laurance, 2008).

Even considering the DSA, we found a significantly negative steeper slope for the *interior* group than for both *generalist* and *edge* species (Fig. 2b). Being less negatively affected by the matrix, *generalist* species may better disperse through it, thus partially overcoming the isolation effect (Andrianarimisa *et al.*, 2000; Renjifo, 2001). In addition, *generalist* species, in contrast with *interior* species, may maintain metapopulations far from source areas because they are able to exploit small forest fragments that lack core areas (Fahrig, 2013). On the other hand, because it was demonstrated that *edge* species increase dramatically in fragmented landscapes (Margules & Milkovits, 1994; Laurance *et al.*, 2002), they are probably not so much affected by large distances from source areas as *interior* species.

Finally, the positive effect of NF on species richness was also found to be significantly higher for *interior* species than for *generalist* and *edge* species. For *interior* species, the higher the number of surrounding fragments, the greater the probability of finding fragments that host a core area, which is the most important limiting factor in making a forest fragment suitable for this specialization group. Additionally, *interior* species were positively influenced by the abundance of surrounding fragments because these can serve as stepping stones for individual movements in a heavily fragmented landscape (Baum *et al.*, 2004) where this group is more disadvantaged than *generalist* and *edge* species (see Fahrig, 2013).

In sum, as expected, our results showed that *interior* species are the ecological group, which is most affected by habitat fragmentation. Therefore, we recommend using *interior* species richness as an indicator for the effect of fragmentation when dealing with open communities.

Indicator species analyses

As mentioned above, species richness might not always be the most valuable proxy for conservation purposes

(Fleishman *et al.*, 2006), even when groups of species with homogeneous ecological traits are considered. For this reason, we determined how each species may be differently associated with different degrees of fragmentation by means of the IndVal analysis. In this way, we were able to identify species, or groups of species, that could act as indicators for particular combinations of spatial covariates concerning landscape fragmentation.

We considered only the first three IndVal groups of species resulting from our analysis to be useful indicators because they were associated with no more than two of the 11 clusters of fragments. To be considered informative, an indicator or a group of indicators should have a significant and relatively high IndVal index value (Legendre, 2013), but should also be linked to a restricted number of clusters. All the species pertaining to the first three IndVal groups appeared to be associated only with fragments located near a source area managed as high forest and sited in archipelago contexts with many patches. However, these three groups differed from each other in their requirements concerning FA. The most demanding IndVal group only includes the European Nuthatch. This species, which is strictly sedentary, has a low dispersal capability and needs large individual territories linked to core area habitats (Van Dorp & Opdam, 1987; Matthysen *et al.*, 1995). Its populations could thus be established only in large fragments relatively close to source areas (cluster NLM-H). The second IndVal group of species was also associated with this cluster, although it was also linked to fragments classified as small (clusters NLM-H and NSM-H). The presence of the species pertaining to the second IndVal group in forest fragments appeared to be limited mainly by dispersal capability because they occur only in large or small fragments near source areas. The presence of these species in fragments near source areas could also be guaranteed in small fragments, provided that they were large enough to allow the establishment of individual territories. On the other hand, the Common Redstart, the only member of the third IndVal group, was found to select only small fragments (cluster NSM-H). This is probably due to a preference of this species for heterogeneous mosaics consisting of an archipelago of patches of mature open forest (Taylor & Summers, 2009), even in moderately urbanized areas (Droz *et al.*, 2015).

These results, as expected, confirmed those obtained from the community analysis: *interior* species are particularly sensitive to fragmentation, which makes them particularly suitable for use as indicators. However, our research demonstrated that, even within this group, different species respond differently to the degree of fragmentation according to their biological traits. In particular, the analysis identified two different groups of *interior* species suitable for use as proxies in two different landscape contexts. Moreover, our results highlighted that even some species not strictly linked to core areas, the Eurasian Jay *Garrulus glandarius* (L., 1758) and the Common Redstart, have biological traits that make

them useful proxies of fragmentation effects, just like the *interior* species pertaining to the second IndVal group.

Because fragment characteristics seem to vary systematically across the three regions (Prealps and Apennines with mainly continuous forests and lowland with highly fragmented forests), it is necessary to exclude the concept that the association between the identified indicator species with fragment characteristics is not simply due to the intrinsic linkage between a species and a geographical region. If a regional effect could drive the species preference for particular clusters, we would expect a strongly different frequency of the species occurrence in the source areas of hills (Prealps and Apennines) or in those of lowlands. However, the species occurrence frequencies within the hilly and lowland source areas are not strongly different for all the indicator species [European Nuthatch: Hills = 0.14, Lowland = 0.12; Short-toed Tree-creeper: H = 0.11, L = 0.14; European Robin *Erithacus rubecula* (L., 1758): H = 0.45, L = 0.33; Marsh Tit *Poecile palustris* (L., 1758): H = 0.29, L = 0.38; Eurasian Jay: H = 0.31, L = 0.14; Common Redstart: H = 0.28, L = 0.14]. Thus, we are quite confident in excluding a regional effect on species cluster selection.

CONCLUSIONS

Our results highlight the strong effect of species specialization in explaining the species distribution in terrestrial ecosystems by means of well-established ecological theories such as that of the IBT. Indeed, the species specialization traits exert a strong influence on species–area relationships and isolation and archipelago effects. Compared with other species, such as the *generalist* species, *interior* species better respond to IBT predictions, which makes them the best possible indicators of the effects of fragmentation. Nonetheless, neither all the *interior* species nor the *generalist* species have the same ecological requirements. Only by considering the biological traits of species (i.e. considering each species independently), did we discover the different associations of species with specific combinations of fragment covariates. This led to the identification of area-limited and/or dispersal-limited species, which may serve as indicators for landscapes with different degrees of fragmentation.

ACKNOWLEDGEMENTS

We thank the General Directorate for Agriculture of the Lombardy Region (D.G. Agricoltura della Regione Lombardia) and the Regional Agency for Agricultural and Forestry Development (ERSAF, Ente Regionale per lo Sviluppo Agricolo e Forestale) for supporting this research. We thank Professor Renato Massa, who first started the breeding birds survey in Lombardy. We are very grateful to Dr Matteo Bonetti for language revision. We also thank three anonymous referees for their useful suggestions that helped improve the paper.

REFERENCES

- Ambuel, B. & Temple, S.A. (1983) Area dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology*, **64**, 1057–1068.
- Andrianarimisa, A., Bachmann, L., Ganzhorn, J.U., Goodman, S.M. & Tomiuk, J. (2000) Effects of forest fragmentation on genetic variation in endemic understory forest birds in Central Madagascar. *Journal für Ornithologie*, **141**, 152–159.
- Arnold, G.W., Steven, D.E. & Weeldenburg, J.R. (1993) Influence of remnant size, spacing pattern and connectivity on population boundaries and demography in Euros *Macropus robustus* living in a fragmented landscape. *Biological Conservation*, **64**, 219–239.
- Bani, L., Massimino, D., Bottoni, L. & Massa, R. (2006) A multiscale method for selecting indicator species and priority conservation areas: a case study for broadleaved forests in Lombardy, Italy. *Conservation Biology*, **20**, 512–526.
- Bani, L., Massimino, D., Orioli, V., Bottoni, L. & Massa, R. (2009) Assessment of population trends of common breeding birds in Lombardy, Northern Italy, 1992–2007. *Ornithological Ecology & Evolution*, **21**, 27–44.
- Baum, K.A., Haynes, K.J., Dilleuth, F.P. & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**, 2671–2676.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B*, **57**, 289–300.
- Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A. & Lindenmayer, D.B. (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, **37**, 517–527. doi:10.1111/ecog.00740.
- Blondel, J., Ferry, C. & Frochor, B. (1981) Point counts with unlimited distance. *Studies in Avian Biology*, **6**, 414–420.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I. & Öckinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2075–2082.
- Brottons, L., Monkkonen, M. & Martin, J.L. (2003) Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *The American Naturalist*, **162**, 343–357.
- Cameron, A.C. & Trivedi, P.K. (1990) Regression-based tests for overdispersion in the Poisson model. *Journal of Econometrics*, **46**, 347–364.
- Clements, F.E. (1916) *Plant succession: an analysis of the development of vegetation*. Carnegie Institution of Washington, Washington.
- Collinge, S.K. (1995) *Spatial arrangement of patches and corridors in the landscape: consequences for biological diversity and implications for landscape architecture*. PhD Thesis, Harvard University, Cambridge, MA.
- Cramp, S. & Simmons, K.E.L. (eds) (2006) *BWPI 2.0.1: Birds of the Western Palearctic interactive (DVD-ROM)*. Oxford University Press/BirdGuides Ltd, London, UK.
- Davies, K.F. & Margules, C.R. (1998) Effects of habitat fragmentation on carabid beetles: experimental evidence. *Journal of Animal Ecology*, **67**, 460–471.
- De Caceres, M. & Legendre, P. (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology*, **90**, 3566–3574.
- De Caceres, M., Legendre, P. & Moretti, M. (2010) Improving indicator species analysis by combining groups of sites. *Oikos*, **119**, 1674–1684.
- Debinski, D.M. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.
- Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press, Cambridge, MA.
- Dondina, O., Orioli, V., Massimino, D., Pinoli, G. & Bani, L. (2015) A method to evaluate the combined effect of tree species composition and woodland structure on indicator birds. *Ecological Indicators*, **55**, 44–51.
- Droz, B., Arnoux, R., Rey, E., Bohnenstengel, T. & Laesser, J. (2015) Characterizing the habitat requirements of the Common Redstart (*Phoenicurus phoenicurus*) in moderately urbanized areas. *Ornis Fennica*, **92**, 112–122.
- Dufrène, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.
- ERSAF (2007) *Destinazione d'Uso dei Suoli Agricoli e Forestali (DUSAF)*. Ente Regionale per i Servizi all'Agricoltura e alle Foreste della Lombardia, Milano.
- ERSAF (2014) *Destinazione d'Uso dei Suoli Agricoli e Forestali (DUSAF)*. Ente Regionale per i Servizi all'Agricoltura e alle Foreste della Lombardia, Milano.
- ESRI (2011) *ArcGIS Desktop: Release 10*. Environmental Systems Research Institute, Redlands, CA.
- Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.
- Fischer, J. & Lindenmayer, J.B. (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**, 265–280.
- Fleishman, E., Noss, R.F. & Noon, B.R. (2006) Utility and limitations of species richness metrics for conservation planning. *Ecological Indicators*, **6**, 543–553.
- Fornasari, L., Bani, L., de Carli, E. & Massa, R. (1998) Optimum design in monitoring common birds and their habitat. *Gibier Faune Sauvage*, **15**, 309–322.
- Franzén, M., Schweiger, O. & Betzholtz, P.-E. (2012) Species-area relationships are controlled by species traits. *PLoS ONE*, **7**, e37359.

- Gascon, C. & Lovejoy, T.E. (1998) Ecological impacts of forest fragmentation in central Amazonia. *Zoology-Analysis of Complex Systems*, **101**, 273–280.
- Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **43**, 463–481.
- Gotelli, N.J. (2008) *A primer of ecology*, 4th edn. Sinauer Associates Inc, Sunderland, MA.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hanski, I. & Gaggiotti, O.E. (2004) *Ecology, genetics and evolution of metapopulations*. Elsevier, Amsterdam, the Netherlands.
- Hanski, I. & Gilpin, M.E. (1997) *Metapopulation biology: ecology, genetics and evolution*. Academic Press, London, UK.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.
- Kleiber, C. & Zeileis, A. (2008) *Applied econometrics with R*. Springer-Verlag, New York. Available at: <http://CRAN.R-project.org/package=AER>. (Accessed 16 May 2016)
- Krauss, J., Steffan-Dewenter, I. & Tschardt, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889–900.
- Laurance, W.F. (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation*, **141**, 1731–1744.
- Laurance, W.F. & Bierregaard, R.O. (1996) Fragmented tropical forests. *Bulletin of the Ecological Society of America*, **77**, 34–36.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H., Bruna, E., Didham, R., Stouffer, P., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology*, **16**, 605–618.
- Legendre, P. (2013) Indicator species: computation. *Encyclopedia of biodiversity*, Vol. 4, 2nd edn (ed. by S.A. Levin), pp. 264–268. Academic Press, San Diego, CA.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H. & Lindenmayer, B.D. (2002) Effects of forest fragmentation of bird assemblage in a novel landscape context. *Ecological Monographs*, **72**, 1–18.
- Mac Nally, R. (2007) Use of abundance spectrum and relative abundance distributions to analyze assemblage change in massively altered landscapes. *The American Naturalist*, **170**, 319–330.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Magura, T., Báldi, A. & Horváth, R. (2008) Breakdown of the species-area relationship in exotic but not in native forest patches. *Acta Oecologica*, **33**, 272–279.
- Margules, C.R. (1996) Experimental fragmentation. *Species survival in fragmented landscapes* (ed. by J. Settele, C.R. Margules, P. Poschlod and K. Henle), pp. 128–137. Kluwer Academic, Dordrecht, The Netherlands.
- Margules, C.R. & Milkovits, G.A. (1994) Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. *Ecology*, **75**, 2033–2042.
- Margules, C.R., Higgs, A.J. & Rafe, R.W. (1982) Modern biogeographic theory: are there any lessons for nature reserve design? *Biological Conservation*, **24**, 115–128.
- Matthews, T.J., Cottee-Jones, H.E. & Whittaker, R.J. (2014) Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, **20**, 1136–114.
- Matthysen, E., Adriaensen, F. & Dhondt, A.A. (1995) Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos*, **72**, 375–381.
- McCullough, D.R. (1997) *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Moran, P.A.P. (1950) Notes on continuous stochastic phenomena. *Biometrika*, **37**, 17–23.
- Morelli, F. (2015) Indicator species for avian biodiversity hotspots: combination of specialists and generalists is necessary in less natural environments. *Journal for Nature Conservation*, **27**, 54–62. doi:10.1016/j.jnc.2015.06.006.
- Naimi, B. (2015) *usdm: Uncertainty analysis for species distribution models*. R package version 1.1-15. Available at: <https://CRAN.R-project.org/package=usdm>.
- Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, J.S. & Bommarco, R. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters*, **13**, 969–979.
- Paton, P.W.C. (1994) The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology*, **8**, 17–26.
- R Development Core Team (2014) *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Renjifo, L.M. (2001) Effect of natural and anthropogenic landscape metrics on the abundance of Subandean bird species. *Ecological Applications*, **11**, 14–31.
- Schemiegelow, F.K.A., Machtans, C.S. & Hannon, S.J. (1997) Are boreal birds resilient to forest fragmentation: an experimental study of short-term community responses. *Ecology*, **78**, 1914–1932.
- Sekercioglu, C.H. & Sodhi, N.S. (2007) Conservation biology: predicting birds' responses to forest fragmentation. *Current Biology*, **17**, R838–R840.
- Simberloff, D. & Abele, L.G. (1982) Refuge designseory: effects of fragmentation. *The American Naturalist*, **120**, 41–50.
- Taylor, S.D. & Summers, R.W. (2009) Breeding numbers and stand type preferences of Redstarts *Phoenicurus phoenicurus* and Tree Pipits *Anthus trivialis* in a Scots Pine *Pinus sylvestris* wood. *Bird Study*, **56**, 120–126.

- Terborgh, J. (1976) Island biogeography and conservation: strategy and limitations. *Science*, **193**, 1029–1030.
- Triantis, K.A. & Bhagwat, S.A. (2011) Applied island biogeography. *Conservation biogeography* (ed. by R.J. Ladle and R.J. Whittaker), pp. 190–223. Wiley-Blackwell, Oxford, UK.
- Triantis, K.A., Economo, E.P., Guilhaumon, F. & Ricklefs, R.E. (2015) Diversity regulation at macro-scales: species richness on oceanic archipelagos. *Global Ecology and Biogeography*, **24**, 594–605. doi:10.1111/geb.12301.
- Van Dorp, D. & Opdam, P.F.M. (1987) Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology*, **1**, 59–73.
- Watling, J.I. & Donnelly, M.A. (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. *Conservation Biology*, **20**, 1016–1025.
- Watson, J.E.M., Whittaker, R.J. & Dawson, T.P. (2004) Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography*, **31**, 1791–1807.
- Wilson, E.O. & Willis, E.O. (1975) Applied biogeography. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 522–534. Harvard University Press, Cambridge, MA.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer Science+Business Media, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Bird classification according to forest specialization groups.

BIOSKETCH

The Biodiversity Conservation Unit of the Department of Earth and Environmental Sciences at the University of Milano–Bicocca focuses on wildlife–habitat relationships, identification and evaluation of ecological networks, forest management practices assessment for animal conservation, wildlife surveys and management, long-term monitoring programs, population and landscape genetics.

Author contributions: O.D. performed statistical analyses and wrote the paper; V.O. performed field survey and statistical analyses; P.D. managed bird and environment data; M.L. performed statistical analyses and L.B. designed and coordinated the study, performed field surveys and wrote the paper.

Editor: Kostas Triantis