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Research Paper

Patch and landscape responses of bird abundance to fragmentation in agroecosystems of east-central Argentina

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ABSTRACT. Forest fragmentation in agroecosystems is linked to declines of avian species worldwide. Agriculture has greatly reduced native forest cover in east-central Argentina. Assessing the influence of fragmentation on forest bird populations is vital to inform reliable conservation and management strategies for the Espinal region of Argentina. We determined the relationships of vegetation structure within native forest patches, size and shape of these patches (patch scale), composition and spatial configuration (at landscape scale) to relative abundance of 17 forest bird species during austral fall-winter and spring-summer seasons. Birds were sampled from 2007–2009 in 45 forest patches within three landscape mosaics (30 x 30 km) representing a gradient of native forest fragmentation in east-central Argentina. We used an information-theoretic approach and approximated model inference to examine the effect of predictor environmental variables at two spatial scales on patterns of forest bird abundance. Density of trees within forest patches was the main predictor of bird abundance at the patch scale. Amount of forest and spatial configuration were also important. The abundance of several bird species was greater in patches with high density of trees and landscapes characterized by more forest cover and larger patches in close proximity. We found two main avian response patterns to forest fragmentation and patch characteristics. This information contributes reliable knowledge for the design of conservation measures of agricultural landscapes in the Espinal region of Argentina.

Abondance d'oiseaux dans les îlots et les paysages à la suite de la fragmentation dans des agrosystèmes du centre-est de l'Argentine

RÉSUMÉ. La fragmentation forestière dans les agrosystèmes est liée à la diminution d'espèces aviaires partout dans le monde. L'agriculture a grandement réduit la superficie de forêts indigènes dans le centre-est de l'Argentine. L'évaluation de l'influence de la fragmentation sur les populations d'oiseaux forestiers est cruciale pour que les gestionnaires puissent choisit des stratégies de conservation et de gestion fiables dans la région de l'Espinal en Argentine. Nous avons déterminé les relations de la structure de la végétation dans les îlots forestiers, de la taille et de la forme de ces îlots (échelle des îlots), de la composition et de la configuration spatiale (à l'échelle du paysage) avec l'abondance relative de 17 espèces d'oiseaux forestiers durant les saisons automne-hiver et printemps-été austraux. Les oiseaux ont été échantillonnés de 2007 à 2009 dans 45 îlots forestiers se trouvant dans 3 mosaïques paysagères (30 x 30 km) représentatives d'un gradient de fragmentation de la forêt indigène dans le centre-est de l'Argentine. Nous avons utilisé une approche fondée sur la théorie de l'information et un modèle d'inférence flou pour examiner l'effet des variables environnementales explicatives sur la tendance de l'abondance des oiseaux forestiers aux deux échelles spatiales. La densité d'arbres dans les îlots forestiers était la principale variable explicative de l'abondance à l'échelle des îlots. La superficie de forêt et la configuration spatiale étaient aussi importantes. L'abondance de plusieurs espèces d'oiseaux était supérieure dans les îlots où la densité d'arbres était élevée et dans les paysages caractérisés par une plus grande superficie de couvert forestier et par de plus grands îlots près les uns des autres. Nous avons trouvé deux types principaux de réaction des oiseaux à la fragmentation forestière et aux caractéristiques des îlots. Ces résultats contribuent à une connaissance plus éclairée en vue d'élaborer des mesures de conservation de paysages agricoles dans la région de l'Espinal en Argentine.

Key Words: *agroecosystem; birds; Espinal; multimodel inference; patch and landscape scales*

INTRODUCTION

Habitat loss and fragmentation as consequences of land use changes are major drivers of global biodiversity loss (Baillie et al. 2004, Renfrew and Ribic 2008). These processes in turn may modify the composition, structure, or function of landscapes (Fraterrigo et al. 2009, Magrach et al. 2011). Further, fragmentation may alter the original configuration of a landscape, generating isolated patches immersed in a frequently hostile matrix (Forman 1995, McComb 1999, Fahrig 2003). Both processes can negatively influence the abundance, movement, and

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dispersal of birds (Mazerolle and Villard 1999, Zurita and Bellocq 2007, Prugh et al. 2008). This may negatively influence demography and long-term persistence of bird populations, and affect key ecological roles of ecosystem function (Lundberg and Moberg 2003, Hanski 2011, Ye et al. 2013).

Forest ecosystems around the world are among the most affected by habitat loss and fragmentation, in many cases driven by the expansion and intensification of agricultural activities (Geist and Lambin 2002, Hoekstra et al. 2005, Gasparri and Grau 2009). In recent decades, the greatest loss of forests worldwide have occurred in the tropics, particularly in South America and Africa where annual rates of forest loss of 0.43% and 0.54%, respectively, have been reported (FAO 2016). With a loss of 297,000 hectares of forest/year (1.1%/year; FAO 2016), Argentina ranked as one of the top 10 countries with the greatest annual net loss of forest area during 2010 to 2015. In the province of Entre Ríos, located in east-central Argentina, the agricultural frontier has greatly expanded, despite soils poorly suited for production (Wilson 2008). Landscape composition and spatial configuration of native Espinal forest have changed during the past century. Forest cover in the province of Entre Ríos decreased from 56% in 1914 to approximately 13.8% at present (Muñoz et al. 2005, De la Fuente and Suárez 2008, Aizen et al. 2009). This has resulted in a subsequent loss of avian diversity in the region (Schrag et al. 2009, Gavier-Pizarro et al. 2012).

Bird species respond differently to environmental changes in fragmented landscapes, exhibiting both negative and positive effects (Antongiovanni and Metzger 2005, Uezu et al. 2005). Generally, negative effects are characterized by population declines from increased mortality, changes in resource availability or nesting sites (Lopez de Casenave et al. 1998, Zanette and Jenkins 2000, Bennett 2003). Fragmentation may also alter bird community structure through reductions of forest interior species, followed by an increase of generalist species associated with edge habitats (Merriam and Wegner 1992). Further, the increased isolation of remnant forest patches may compromise movement of species with reduced dispersal ability with potential negative consequences when remnant forest patches are immersed in a matrix of unsuitable habitat (Lens et al. 2002, Şekercioglu et al. 2002). Consequently, spatial scale plays a prominent role in the response of bird species to fragmentation (Holland and Bennett 2009).

The spatial scales at which birds respond to environmental characteristics may have conservation and management implications (Holland and Bennett 2009). For example, within patch, i.e., tree density and height, and patch-scale, i.e., patch size, features have been linked to population abundance and community structure of forest birds (Forman 2006, Skórka et al. 2016). Alternatively, factors characterizing the surrounding matrix can determine the main effects on bird community structure and composition (Gascon et al. 1999, Ribic and Sample 2001, Horn and Koford 2006). These hierarchal, i.e., patch to landscape, responses reflect the various environmental components required by forest birds to maximize fitness and complete their annual cycle (Manning et al. 2004, Thornton et al. 2011). Assessing the degree of sensitivity or tolerance at patch and landscape scales can provide insight into the effects of agriculture expansion on native forest birds. If we compare and integrate agricultural landscapes that represent a gradient of changes that occurred during the fragmentation process, trading space for time, we can determine bird response to agricultural expansion (dos Anjos 2006, Şekercioglu and Sodhi 2007).

Agricultural expansion is expected to continue in the province of Entre Ríos with consequent alterations to native forest cover and configuration. Therefore, it is important to assess the influence of this multiscale process on one of the better indicators of ecological conditions, namely, native forest birds (Canterbury et al. 2000, O'Connell et al. 2000). In this study we analyzed the effect of forest fragmentation at patch and landscape scales on birds in east-central Argentina. Our objectives were to examine relationships between relative abundance of birds and environmental characteristics at patch and landscape scales and identify predictor variables influencing bird abundance. We predicted response by native forest birds to fragmentation in our study landscape would be a function of degree of habitat specialization and would differ by individual species along an autoecological gradient from sensitive to tolerant. Further, we predicted relative abundance of forest bird species would reflect variability of site-specific differences in patch characteristics. We used predictive habitat models to relate bird abundance to environmental characteristics of fragmented forest landscapes to assess their use for conservation planning (Mazerolle and Villard 1999, Henle et al. 2004, Thornton et al. 2011).

METHODS

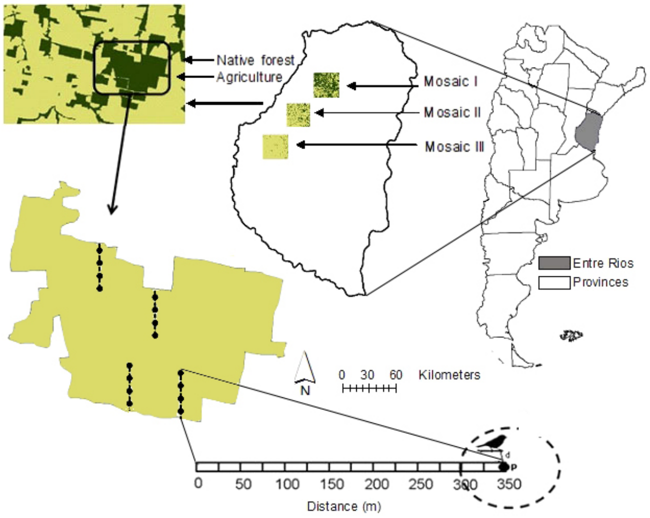
Study area

We conducted our study in the departments of Paraná, Diamante, Nogoyá, and La Paz of Entre Ríos province located in eastern Argentina. Entre Ríos is found within the Espinal ecoregion (Cabrera 1994). The Espinal ecoregion is characterized by semixerophytic forests dominated by hardwood tree species such as *Prosopis affinis, Acacia caven, Geoffroea decorticans,* and *Celtis ehrenbergiana* (Lewis et al. 2009, Matteucci 2012). Mean annual temperature is 18–20 °C and precipitation ranges from 800 to 1000 mm. Topography of the landscape is mostly flat plains interspersed with smooth undulations. The current state of Espinal forest remnants is the outcome of a process of secondary succession. Anthropogenic disturbances originated by indigenous peoples approximately 2000 years ago, but deforestation substantially intensified during the last 200 years. The most important changes in vegetation have occurred since the beginning of the 20th century, mainly from cattle ranching followed by industrial agriculture, mostly soybean (Muñoz et al. 2005, Engler and Vicente 2009, Matteucci 2012).

We placed a grid with a cell size of 30 x 30 km in each of the provincial departments encompassing our study area using a Geographic Information System. We classified all cells, using visual interpretation, according to the proportion of native forest cover into three categories (> 50%, 15–50%, < 5%), then randomly selected one cell for each category. The selected landscape mosaics represented a gradient of forest fragmentation resulting from agricultural expansion processes (Fig. 1). Mosaic I (31°20'31.5" S, 59°26'43.2" W) included 54% native forest cover interspersed with agricultural patches. Mosaic II (31°34'52.2" S, 60°04'29.3" W) was dominated by an agricultural matrix with 23% forest cover connected by corridors of riparian forest. Finally, mosaic III (32°

02'2.6" S, 60°18'29.9" W) was dominated by intensive crop agriculture with interspersed forest fragments representing 4% of the total area.

Fig. 1. Map of Argentina indicating location of Entre Ríos province and study mosaics. Detail of sublandscape with highlighted forest patch (dark green areas) and outline of bird sampling points within forest patch.



Each landscape mosaic was subdivided into nine nonoverlapping 10 x 10 km cells using ArcGIS version 9.2 (Esri, Redlands, CA, USA). We randomly selected six cells, hereafter termed sublandscapes. Within each sublandscape we randomly selected forest patches in three size categories (< 7 ha, 8–20 ha, > 21 ha), 15 in each mosaic for a total of 45 patches. A forest patch was defined as a contiguous area covered by native forest that differed from its surroundings. Average size of these 45 native forest patches (± standard error) was 37.16 ± 5.25 ha. However, mean patch area was 253.95 (± 40.03), 64.36 (± 12.85), and 15.12 (± 4.19) for mosaics I, II, and III, respectively. Following a first visit to each patch, we planned our bird and vegetation structure sampling scheme.

Bird community

We sampled forest birds during the austral seasons of fall-winter 2007 and 2008 (May to July) and spring-summer 2007–2009 (November to January). We selected 19 diurnal, terrestrial bird species to derive abundance estimates (Table A1.1). Selected taxa were common species representative of the Espinal forest region (Narosky and Yzurieta 2010). Further, selected species illustrated a diversity of foraging guilds, e.g., insectivores and granivores, and habitat use preferences of varying forest strata (understory, midstory, canopy). Common and taxonomic names of bird species followed De la Peña and Rumboll (1998).

We used 10-minute circular point counts (50-m radius) to estimate relative abundance, expressed as number of birds per point per patch (Savard and Hooper 1995, Bibby et al. 2000). We randomized distance between transects and placed points along transects perpendicular to the edge of each forest patch. The number of points on a given transect was proportional to patch size (range = 4–16 points per patch) and points were located at a minimum distance of 100 m to decrease the possibility of double counting (Bibby et al. 2000; Fig. 1). Surveys were conducted between 0600–1000 h (spring-summer), 0700–1100 h (fall-winter) or 1500–1900 h (spring-summer), 1400–1800 h (fall-winter), with one patch sampled per morning–afternoon period. We visited each point once per season. Surveys were not conducted during rainy or windy days (wind ≥ 20 km/h). During the first set of surveys, the number of observations was greater in the morning block (= 253, SE = 69.30) compared to the afternoon (= 181, SE = 29.79). Therefore, we kept the same block observation in the first two surveys and reversed the block schedule in the last two surveys. This decision was made to avoid masking possible seasonal influences on bird detections (Bibby et al. 2000). We attempted to estimate detection functions for all bird species in native forest patches based on distance data and following Buckland et al. (2001). However, for most species this approach was not feasible primarily because of an insufficient number of independent detections to fit the detection function, thus violating a key assumption of distance sampling. Therefore, abundance estimates were reported as relative abundance ± standard error.

Patch-scale variables

We selected vegetation structure variables to measure characteristics within forest patches based on the literature (García Del Rey and Cresswell 2005, Johnston and Holberton 2009). We used the dot-quadrant method (Cottam and Curtis 1956) at each point to quantify tree density (D_Arb) and shrub density (D_arb) as number of trees/shrubs per hectare. We also documented additional measures collected from the tree closest to the center of the plot in each quadrant, including tree height (A_Arb) using a clinometer (Romahn de la Vega et al. 1994), and diameter at breast height (DBH). These measures were averaged over all sampling points in a patch to obtain a single value representing patch scale vegetation structural variables.

We considered additional patch level variables known to affect bird populations (i.e., breeding habitat), community structure, or spatial and temporal distribution (Estades 2001, Graham and Blake 2001, Suarez-Rubio and Thomlinson 2009). These included patch area (PA), total edge (TE), shape index (SI), perimeter-area ratio (PARA), fractal dimension (FD), linear distance of patch to nearest settlement (DistLoc), latitude (X), and longitude (Y) for the central point of each forest patch (Gauss-Kruger, zone 5). The last two variables were included in the analysis to account for potential landscape scale spatial patterns masking relationships between bird abundance and patch characteristics, and account for potential correlation of other variables responding to the same landscape scale gradients.

Variables were measured using Quickbird images (available in Google Earth™ http://earth.google.com) and the Patch Analyst extension for ArcGIS (Rempel et al. 2012). These described the amount and configuration of each forest patch beyond those that described environmental characteristics within patches. Possible correlations among patch scale variables were tested using a Pearson's matrix and discarded variables that showed high levels of correlation (r ≥ 0.70, P < 0.05; Table 1).

Table 1. Correlation matrix for forest patch scale variables. D_Arb = Density of trees, D_arb = Density of shrubs, A_Arb = Tree height, DBH = Diameter at breast height, PA = Forest patch area, TE = Total edge, SI = Shape index, PARA = Perimeter-area ratio, FD = Fractal dimension, DistLoc = Lineal distance from forest patch to nearest settlement.

	D_Arb	D_arb	A_Arb	DBH	DistLoc	X†	Y‡	PA	TE	SI	PARA
D_Arb											
D_arb	0.23										
A_Arb	0.25	-0.12									
DBH	0.03	-0.22	0.63								
DistLoc	-0.12	-0.15	-0.35	-0.01							
X	0.28	0.26	-0.28	-0.08	0.26						
Y	0.52	0.30	-0.10	0.05	0.20	0.89*					
PA	0.14	0.35	0.12	-0.10	-0.23	0.01	0.03				
TE	0.04	0.29	0.17	-0.06	-0.19	-0.15	-0.13	0.89*			
SI	-0.22	0.02	0.17	0.02	-0.05	-0.39	-0.36	0.34	0.70*		
PARA	-0.24	-0.27	-0.12	0.11	0.26	0.01	0.01	-0.67	-0.63	-0.08	
FD	-0.37	-0.26	0.03	0.11	0.18	-0.32	-0.30	-0.40	-0.10	0.60	0.72*

*P = 0.05
X†= latitude
Y‡= longitude

Landscape-scale variables

We quantified amount and spatial configuration of forest cover in each sublandscape using reference satellite images (Landsat Thematic Mapper, 5) of 30-m spatial resolution (Path 226-Row 82, January 2007-2008). Images were downloaded from the Brazilian National Institute for Space Research (INPE) web site. Thermal bands were not retained because of coarser resolution. Images were geometrically corrected using a first-degree polynomial model given study area topography. Images were orthorectified using a digital elevation model (DEM, 30-m spatial resolution) and nearest neighbor as a resampling method. Vector topology was reconstructed using a PAEK algorithm (polynomial approximation with exponential Kernel) with a 50 m tolerance (Menéndez and La Roca 2007), then vectors rasterized (5-m cell size) in ArcGIS.

Landsat™ satellite images were classified with support vector machines (SVM), a nonparametric supervised classification algorithm (van der Linden et al. 2009). The SVM approach distinguishes classes by fitting separating hyperplanes in feature space based on training samples (Foody and Mathur 2004). After training sites were digitized, statistical characterizations were derived and 10 land use-cover types identified: water bodies (W), corn (C), sunflower (S), soybean (S), sorghum (So), other crops (Oc) included annual and perennial pastures and fields with weeds, introduced forest (Pf), native forest (Fn), flooded vegetation (Vf) and urban-bare soil (URS).

We trained the SVM using 250 randomly selected pixels of each class. Although the SVM approach was originally developed for binary classifications, we worked with multiclass images overcoming that problem through a one-against-one approach that applied a set of individual classifiers to all possible class pairs and performed a majority vote to assign the winning class (Huang et al. 2002, Pal and Mather 2005). Further, we determined magnitude of penalty given to misclassified training data (C) and width of the Gaussian kernel function selected (γ). Once optimal parameters were found, we used the resulting SVM to classify the images (Janz et al. 2007, Kuemmerle et al. 2008). We eliminated pixel groups smaller than 0.81 ha (3 x 3 pixels) representing classification artifacts or areas without ecological importance to the scale of our study. We validated classification results with 100 randomly selected points per land class type using Quickbird images and ground truthing (Congalton and Green 2009). Overall classification accuracy was 82% (2007) and 84% (2008; Table A2.1).

We estimated forest fragmentation in each sublandscape by calculating metrics that quantified amount and edge of forest cover, namely total forest area in each mosaic (FA, A3.1), number of forest patches (NP, A3.2), mean patch area (PA, A3.3), and edge density (ED, A3.4). Additionally these metrics described shape complexity of forest patches with measures of shape index (SI, A3.5), fractal dimension index (FD, A3.6), and perimeter-area ratio (PARA, A3.7). Finally, they addressed spatial configuration of the forest via mean distance (Euclidean) to nearest neighbor patch (ENN, A3.8), patch cohesion index (COH, A3.9), and aggregation index (AI, A3.10). These are considered robust metrics for fragmentation measurements and allow the definition of patterns (Wang et al. 2014). When constructing our models, we averaged metrics for 2007 and 2008 as there was no difference among years ($P > 0.05$). We used area of each cover type, contagion (CO), interspersion and juxtaposition (IJI), and richness (PR) to characterize the surrounding matrix on each sublandscape. All landscape-scale metrics were calculated using FRAGSTATS version 4 (McGarigal et al. 2012).

Analysis

We used Kruskal Wallis tests ($P > 0.05$) to evaluate differences at patch and landscape scale variables between mosaics. The relationships between the environmental metrics selected to characterize forest patches indicated variables PA and TE were highly correlated (Table 1). Therefore, we selected PA for model building given its wide use in other studies of species-habitat relationships (Munguía-Rosas and Montiel 2014). Variables describing forest patches PARA and FD were also strongly correlated. Therefore, we included only FD in our models because this index reflects shape complexity across a range of spatial scales (patch sizes; McGarigal et al. 2012; Table 1). We discarded X and Y given these were autocorrelated, although were uncorrelated with any of the other explanatory variables. Therefore, this discards any possible spatial patterns of patch scale variables along the landscape fragmentation gradient. Further, we used a correlation approach to examine relations among cover type metrics at the landscape scale. Because forest cover landscape metrics were correlated ($r \geq 0.70$, $P < 0.05$; Table 2), we used a principal components analysis (PCA) to obtain independent measurements of these variables (McCune et al. 2002). The resulting two vectors accounted for 86% of the variance in the original data matrix (PC1 63%, PC2 23%). Axis PC1 represented a gradient of sublandscapes dominated by large patches of connected forest with less edge and simpler shapes to sublandscapes with reduced forest cover characterized by smaller patches of forest with greater edge and complex shapes. Axis PC2 represented a gradient of covariation among sublandscapes with low number of large patches to sublandscapes with greater number of smaller patches and finally, sublandscapes characterized by low patch number of small size.

Table 2. Correlation matrix of spatial metrics for amount and spatial configuration of forest cover of sublandscapes (10 x 10 km). FA = Total forest area (ha), NP = Number of patches, ED = Edge density, PA = Mean patch area, SI = Shape index, FD = Fractal dimension, PARA = Area-perimeter ratio, ENN = Mean euclidean nearest neighbor patch distance, COH = Patch cohesion index, AI = Aggregation index.

	FA	NP	ED	PA	SI	FD	PARA	ENN	COH
NP	0.09								
ED	0.84*	0.49							
PA	0.94*	-0.14	0.71*						
SI	-0.62	-0.63	-0.79*	-0.48					
FD	-0.71*	-0.53	-0.83*	-0.58	0.92*				
PARA	0.53	-0.43	0.14	0.70*	0.06	0.00			
ENN	-0.50	-0.50	-0.68	-0.40	0.85*	0.63	0.11		
COH	0.81*	0.27	0.90*	0.70*	-0.65	-0.73*	0.20	-0.60	
AI	0.62	0.53	0.79*	0.50	-0.92*	-0.78*	-0.06	-0.96*	0.75*

*P = 0.05

Relative abundance of each bird species per season was modeled as a function of patch and landscape variables. We built two sets of models independently. These included models where patch variables were considered, and models with landscape variables only. We selected this approach given differences in sample sizes, with 45 patches for the first set of models and 18 (six sublandscapes in each of three mosaics) at the landscape scale. Based on this criterion, each model included only one to three explanatory variables.

The response variable (relative bird abundance) and explanatory variables (patch and landscape metrics) were examined graphically and analytically for multicollinearity and deviation from normality using Infostat (Di Rienzo et al. 2010). We then used generalized linear models (GLM; Guisan et al. 2002, Seavy et al. 2005) with a Gaussian error structure (log-transformed when condition was not met) to examine the influence of environmental variables on relative abundance of each bird species using package glm in program R ver.2.14 (R Development Core Team 2013). We first constructed models for each single variable, followed by models with sets of two and three variables within each model set (Table A4.1). We used this exploratory approach, rather than a more restricted set of a prior models (Fletcher and Koford 2002) given the absence of prior information on the explanatory power of our variables. We used Akaike's information criteria adjusted for small sample size (AICc) to compare model performance and considered Δ AICc scores ≤ 2 to be competitive models (Burnham and Anderson 2002).

For each spatial scale analyzed we used model averaging and sum of weights of competitive models where a variable was present ($\Sigma\omega i$; Burnham and Anderson 2002) to evaluate individual variable performance at each scale (patch and landscape). Variables with a value of $\Sigma\omega i$ close to 1 were the most important predictor variables. Additionally, we used a hierarchical partitioning analysis to calculate the percent variance of the full model explained by each variable when all other variables were included in the model. For estimates of avian abundance, we fitted all possible models based on different combinations of the explanatory variables. For each fitted model the variable of interest was removed before refitting the model. Variable importance was calculated as the average change in R^2 when a variable was removed from all fitted models (MacNally 2002). Finally, we assessed spatial autocorrelation using randomized semivariograms of model residuals (Isaaks and Srivastava 1989). There was no evidence of a spatial autocorrelation effect in our models.

RESULTS

Bird species abundance

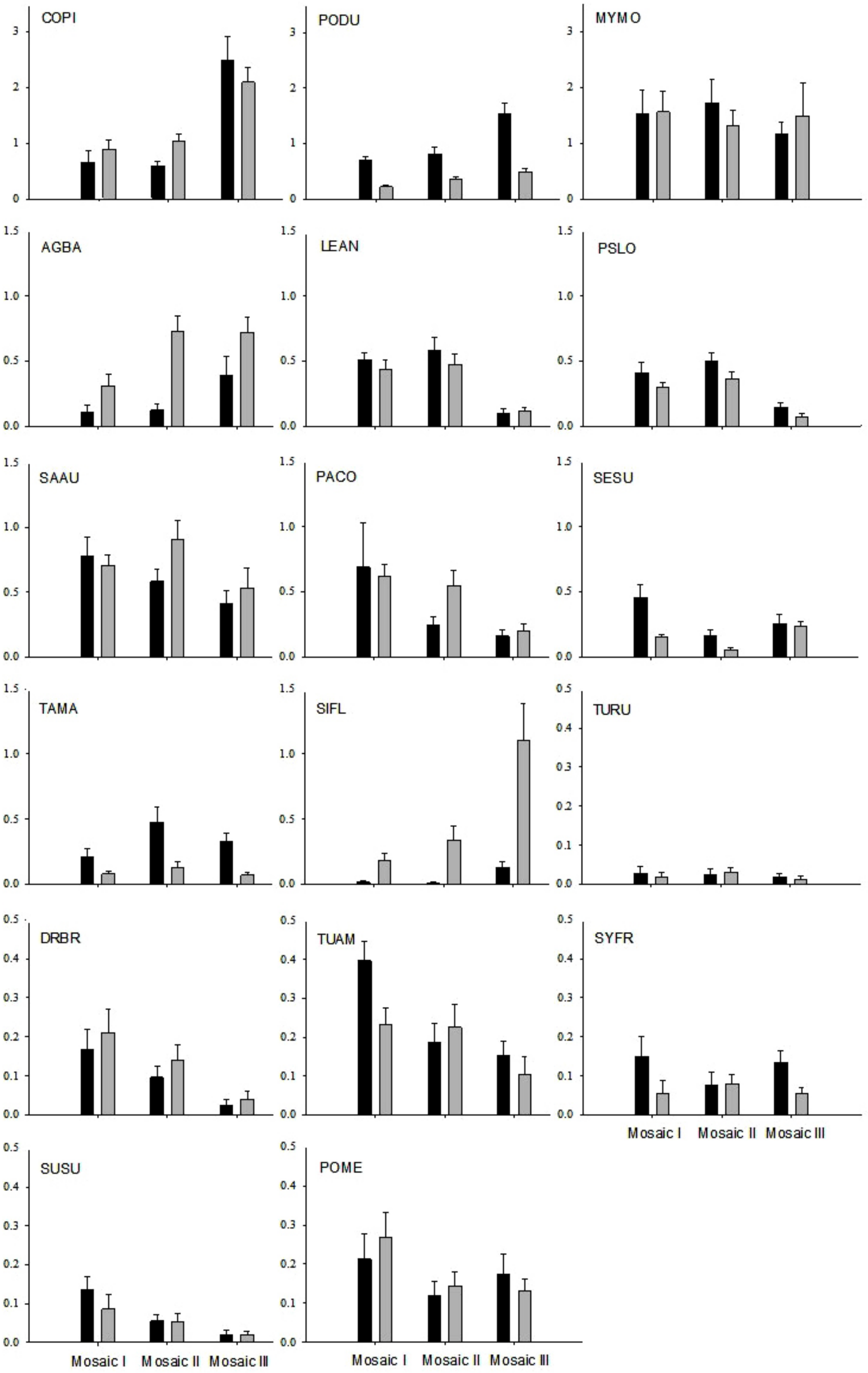
We removed Greyish Saltator (*Saltator coerulescens*) and Short-billed Canastero (*Asthenes baeri*), from subsequent analysis because of the low number of detections. Relative abundance estimates differed for most species by season (fall-winter, spring-summer) and landscape mosaic (Fig. 2). Picui Ground Dove (*Columbina picui*) and Monk Parakeet (*Myiopsitta monachus*) were the most abundant species in forest patches. Relative abundance of Picui Ground Dove was 1.24 ± 0.21 individuals per point per patch during fall-winter and 1.47 ± 0.25 per point per patch during spring-summer. Monk Parakeet relative abundance was 1.34 ± 0.21 per point per patch in fall-winter, and 1.45 ± 0.25 per point per patch in spring-summer.

Mosaic I, characterized by the greater amount of forest cover, contained greater abundances of Scimitar-billed Woodcreeper (*Drymornis bridgesii*), Creamy-bellied Thrush (*Turdus amaurochalinus*), Red-crested Cardinal (*Paroaria coronata*), Suiriri Flycatcher (*Suiriri suiriri*), and Black-capped Warbling Finch (*Poospiza melanoleuca*). Conversely, Great Antshrike (*Taraba major*) and Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*) were more abundant in mosaic II, while the most abundant species in mosaic III included Picui Ground Dove, Grayish Baywing (*Agelaioides badius*), Saffron Finch (*Sicalis flaveola*), and Masked Gnatcatcher (*Polioptila dumicola*; Fig. 2).

Mosaic description

As expected, tree density was greater in mosaic I (= 355 ± 36 indiv/ha) and mosaic II (= 451 ± 25 indiv/ha) compared with mosaic III (= 166 ± 29 indiv/ha, Table A5.1). However, tree height was greater and statistically significant only in mosaic II (= 5.40 ± 0.18

Fig. 2. Relative abundance (no. indiv/point/patch) of birds in forest patches sampled in landscape mosaics of Entre Ríos province, Argentina, during fall-winter (black) and spring-summer (gray) of 2007–2008.



m) compared with mosaic I (= 4.44 ± 0.18 m). Shrub density did not differ between mosaics (mosaic I = 528 ± 84 indiv/ha, mosaic II = 462 ± 79 indiv/ha and mosaic III = 289 ± 44 indiv/ha). Forest amount and configuration differed ($P < 0.05$) between mosaics. Mosaic I was dominated by continuous forest cover while mosaic III had the lowest amount of forest (Table A5.1). Mosaic I was mainly characterized by 54% native forest, 38% annual crops, whereas mosaic II had 23% native forest, 66% annual crops, and finally mosaic III had 4% native forest and 77% annual crops. Additionally, mosaic II had the greater number of forest patches indicating an intermediate stage in the fragmentation process, whereas mosaic III had the lowest number of patches; its mean area was also the lowest and its mean shape of patches was the most complex (Table A5.1).

We observed that some variables presented associations among spatial scales, despite evaluating relationships between bird abundance and environmental metrics at both patch and landscape scales using independent sets of models (Table A6.1). On the one hand, these associations indicated that patches with greater tree height were found in landscapes characterized by a greater number of patches. On the other hand, the shape complexity of the 45 sampled patches was positively associated with the shape pattern at landscape scale. Finally, the landscapes characterized by greater number of forest patches (included in axis PC2) were also characterized by the more disaggregated land use-cover types (Table A6.1).

Patch and landscape scales bird response

Although the response to forest fragmentation varied among avian species, we identified two main patterns: (1) species sensitive to vegetation structure conditions within patch and forest fragmentation (e.g., Narrow-billed Woodcreeper, Scimitar-billed Woodcreeper, and Brown Cacholote (*Pseudoseisura lophotes*), and (2) tolerant species (e.g., Picui Ground Dove, Saffron Finch, and Masked Gnatcatcher).

Vegetation structural variables were incorporated in most individual bird models (Table 3). Number of trees per hectare was important when determining abundance of bird species during both seasons. Variables related to tree size (DBH and A_Arb) were not as important as tree density (Table 4). Tree height had a strong and positive effect on several species including Sooty-fronted Spinetail (*Synallaxis frontalis*), Great Antshrike, Creamy-bellied Thrush, Golden-billed Saltator (*Saltator aurantiirostris*) and a negative effect on White-crested Tyrannulet (*Serpophaga subcristata*), Saffron Finch, and Monk Parakeet. Shrub density had a clear negative effect on only three species; Rufous-bellied Thrush (*Turdus rufiventris*), Grayish Baywing, and Picui Ground Dove. The abundance of Narrow-billed Woodcreeper, Scimitar-billed Woodcreeper, Great Antshrike, and Creamy-bellied Thrush increased proportionally with density of trees within forest patches. Conversely, Grayish Baywing, Picui Ground Dove, Black-capped Warbling Finch, and Saffron Finch were more abundant in patches with lesser tree densities (Table 3).

Variables characterizing patch shape complexity, such as shape index (SI) and fractal dimension (FD) were incorporated in most individual bird models during both seasons (Table 3). Furthermore, relative importance based on model weights of SI (range = 0.28–0.98) and FD (range = 0.24–1.00) was greater for most bird species (Table 4). For example, Scimitar-billed Woodcreeper, Narrow-billed Woodcreeper, Grayish Baywing, Red-crested Cardinal, and Brown Cacholote were more abundant in patches of simpler shape and lesser ratio of edge to forest interior. Conversely, Picui Ground Dove, Great Antshrike, Saffron Finch, Sooty-fronted Spinetail, Masked Gnatcatcher, and Golden-billed Saltator were more abundant in patches of greater shape complexity and greater ratio of edge to forest interior. Proximity to population settlements did not have a clear effect on any bird species, except for Monk Parakeet that was clearly favored by closeness to settlements (Table 3).

Birds also responded to amount and spatial configuration of forest at landscape scale as forest fragmentation metrics were present in the best models (Table 3). Variables summarized by PC1 exhibited greater mean relative importance (0.68) than variables summarized by PC2 (0.41; Table 4). Furthermore, PC1 was found in most species landscape scale models. The relationship of individual bird species to PC1 varied depending on their affinity to forest habitat, ranging from species that feed, reproduce, and nest within the forest, i.e., forest specialists, to open habitat generalists that use the forest, but also the surrounding matrix. Conversely, PC2 was selected in a smaller number of models, some of these included bird species that exhibited a positive response to landscapes with greater number of patches of native forest, e.g., Grayish Baywing, Great Antshrike, and Rufous-bellied Thrush, while other species such as Black-capped Warbling Finch, Creamy-bellied Thrush, White-crested Tyranulet, and Monk Parakeet responded negatively (Table 3).

Finally, the surrounding matrix influenced many bird species such as the Golden-billed Saltator, who exhibited a positive effect of interspersion and juxtaposition (IJI), and whose abundance was greater in landscapes where patch types were close together. Conversely, other species were negatively influenced by IJI including the Scimitar-billed Woodcreeper and White-crested Tyranulet (Table 3). On the other hand, abundance of Rufous-bellied Thrush and Monk Parakeet was positively associated to contagion, and was greater in landscapes where all patch types were aggregated, while Narrow-billed Woodcreeper, Sooty-fronted Spinetail, and Creamy-bellied Thrush had a negative response to CO (Table 3). Finally, the abundance of Grayish Baywing, Red-crested Cardinal, and Brown Cacholote was greater in landscapes with fewer types of different land use-cover (PR; Table 3). Nevertheless, relative importance ($\Sigma\omega i$) of landscape predictor variables describing the matrix was low (< 0.5; Table 4).

DISCUSSION

Forest structure, amount, and spatial configuration successfully explained patterns of bird abundance in fragmented landscapes of the Espinal region in east-central Argentina. Although some species exhibited no apparent response or a positive response to fragmentation, a subset of bird species responded negatively to these patterns at both patch and landscape scales. Thus, potential changes in bird communities in east-central Argentina could be driven by reduced abundance of forest sensitive species. This in turn may enhance the potential for population declines, including local extinctions, as landscapes become increasingly fragmented and simplified (Boulinier et al. 2001). These results were

Table 3. Best generalized linear models describing bird abundance in forest patches during the austral fall-winter and spring summer, in the province of Entre Ríos, Argentina. Parentheses indicate a negative relationship to bird abundance.

Species[†]	Season[‡]	Model					
		Patch[§]	AICc	Akaike weight (ωi)	Landscape[|]	AICc	Akaike weight (ωi)
COPI	FW	(-D_Arb) + (-D_arb)	117.46	0.36	PC1	30.52	0.37
	SS	(-D_Arb) + (-D_arb)	114.42	0.28	PC1	40.33	0.27
AGBA	FW	(-D_Arb)	112.09	0.32	(-PR)	42.27	0.32
	SS	(-D_arb)	61.92	0.36	PC2 + (-PR)	13.54	0.20
DRBR	FW	(-SI)	-47.41	0.57	(-PC1) + (-IJI)	-40.63	0.49
	SS	(-SI) + (-DF) + D_Arb	-27.78	0.38	(-PC1)	-24.19	0.19
LEAN	FW	D_Arb + (-SI) + (-FD)	13.95	0.39	(-PC1) + (-CO)	1.41	0.44
	SS	D_Arb + DBH	6.80	0.69	(-PC1) + (-CO)	-2.54	0.50
SYFR	FW	FD + A_Arb	-51.00	0.77	PR	-23.83	0.16
	SS	FD + A_Arb	46.46	0.57	(-CO)	12.94	0.20
PSLO	FW	(-SI)	12.52	0.49	(-PC1) + (-PR)	-4.89	0.31
	SS	D_Arb + (-SI) + (-FD)	-15.81	0.26	(-PC1)	-13.45	0.37
TAMA	FW	D_Arb + A_Arb + SI	20.25	0.52	PC2	8.95	0.21
	SS	D_Arb + A_Arb + SI	-75.22	0.78	PC2	-34.65	0.15
PODU	FW	(-D_Arb)	83.37	0.37	PC1	12.33	0.34
	SS	(-D_Arb)	-6.24	0.61	PC1	-20.03	0.33
TURU	FW	(-D_arb) + D_Arb	-127.47	0.56	PC2 + CO	-9.97	0.27
	SS	D_Arb	-153.84	0.39	PC2 + CO	-71.88	0.23
TUAM	FW	DistLoc	-13.30	0.34	(-PC1) + (-PC2)	-24.22	0.47
	SS	A_Arb + (-DBH)	-18.31	0.32	(-PC1) + (-CO)	-14.38	0.30
SAAU	FW	D_Arb + A_Arb	63.45	0.26	(-PC1) + IJI	15.80	0.31
	SS	D_Arb + A_Arb + (-DBH)	60.85	0.32	(-PC1) + IJI	21.72	0.33
PACO	FW	(-SI)	118.48	0.34	(-PC1)	34.75	0.33
	SS	(-SI)	43.38	0.51	(-PC1) + (-PR)	3.97	090
POME	FW	(-D_Arb) + (-DBH)	-19.70	0.91	(-PC 2)	-16.02	020
	SS	PA + (-SI) + FD	-33.21	0.98	(-PC1)	-20.01	025
SUSU	FW	(-FD)	-88.69	0.57	(-PC1)	-45.33	0.32
	SS	PA + (-FD)	44.09	0.45	(-PC1)	6.47	0.15
SESU	FW	(-A_Arb)	15.32	0.48	(-IJI)	-6.50	0.24
	SS	(-D_Arb)	-55.90	0.48	PC1 + (-PC2)	-39.13	0.81
SIFL	FW	(-D_Arb) + (-A_Arb)	63.29	0.22	PC1	14.59	0.31
	SS	(-D_Arb) + (-A_Arb) + DBH	114.85	0.38	PC1	39.92	0.35
MYMO	FW	(-A_Arb) + DBH	161.96	0.41	CO	60.82	0.19
	SS	(-DistLoc)	141.20	0.31	(-PC2)	51.74	0.17

[†] Codes of bird species listed in Table A1.1.

[‡] FW = fall-winter, SS = spring-summer.

[§] Patch-scale variables: D_Arb = density of trees, D_arb = density of shrubs, A_Arb = tree height, DBH = diameter at breast height, PA = patch area (ha), SI = Shape index, FD = fractal dimension, DistLoc = linear distance (m) to nearest settlement.

[|] Landscape spatial configuration variables: PC1 = fragmentation gradient principal component, PC2 = fragmentation covariate principal component, IJI = interspersion and juxtaposition, CO = Contagion, and PR = cover type richness.

consistent with other published reports (Gehring and Swihart 2003, Cunningham and Johnson 2006, Thornton et al. 2011) on avian responses to forest fragmentation. Additionally, our results highlighted the importance of evaluating species-habitat relationships at multiple, i.e., patch and landscape, scales because factors varied in importance depending on the spatial scale. For instance, at the patch scale, vegetation structure within patches was comparatively more important than patch shape and size, while at the landscape scale the amount and spatial configuration of native forest cover were comparatively more important than composition and configuration of all cover types present in the landscape.

Vegetation structure within patches was an important predictor for many species in our study, similarly to patterns reported for other regions of the world (Martin 1998, Forman 2006). Tree density within patches was strongly associated (positively or negatively) with 15 out of 17 bird species in our study during both fall-winter and spring-summer. Increased density of trees would benefit cavity nesting species like the Narrow-billed Woodcreeper and Scimitar-billed Woodcreeper by increasing the availability of potential nesting and foraging sites, suggesting these species may be associated to particular forest patch conditions (Nadkarni and Longino 1990, Berg et al. 1994, Cockle et al. 2012). Interestingly, these results differed from studies conducted in North America where an inverse relationship to tree density has been reported for cavity nesting birds (Flack 1976, Brawn 1988). Most North American cavity nesters are more abundant in mature forests dominated by larger trees (and lower tree density), probably because older forests tend to have more dead trees and dead branches on live trees where cavities may be excavated or utilized. Many other species are secondary cavity nesters and rely on abandoned woodpecker nests or natural cavities. In the Espinal forest, bird species that nest in tree cavities are secondary users,

Table 4. Relative importance of spatial metrics at patch and landscape scales based on sum of model weights (Σωi, for each predictor variable shows the sum of Akaike weights for all possible models in which the predictor variable was incorporated at each level) and hierarchical variance partitioning (HP, percent of variance of the full model explained by each variable) for bird species sampled during the austral fall-winter and spring-summer, in the province of Entre Ríos, Argentina.

Species[†]	Season[‡]	Patch[§]																Landscape[ǀ]									
		D_Arb		D_arb		A_Arb		DBH		PA		SI		FD		DistLoc		PC1		PC2		IJI		Contagion		PR	
		Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP	Σωi	HP
COPI	FW	1.0	47.0	0.5	16.6									0.3	9.0			0.9	64.1								
	SS	0.9	44.8	0.5	19.8									0.5	19.9			0.8	42.2								
AGBA	FW	1.0	68.4							0.2	3.7	0.3	7.0	0.3	4.5											0.3	58.7
	SS	0.5	13.7	0.6	46.3															0.4	44.7					0.2	12.7
DRBR	FW											1.0	37.6	0.4	29.2			0.5	44.6			0.5	17.0				
	SS	0.6	8.1			0.3	18.7	0.3	11.3			0.7	14.0	0.5	26.9			0.6	40.4	0.2	7.3			0.4	38.0		
LEAN	FW	1.0	41.2	0.5	0.6	0.8	12.9	0.4	10.2			0.4	19.0	0.4	11.8			0.8	66.1					0.4	9.7		
	SS	1.0	24.6			0.3	11.7	1.0	30.2									0.8	54.1			0.2	20.5	0.5	12.0		
SYFR	FW					0.8	19.8							0.9	46.9											0.2	41.2
	SS					1.0	58.3							0.6	13.0					0.3	16.5			0.4	22.6		
PSLO	FW											1.0	42.9	0.5	31.4			0.6	15.2							0.3	58.7
	SS	0.7	30.7			0.2	6.7	0.2	15.8			0.5	16.1	0.4	23.5			0.7	57.0								
TAMA	FW	0.8	13.5			0.9	42.3					0.7	17.3							0.4	30.5	0.2	30.4	0.2	26.1		
	SS	0.8	18.7			1.0	33.0					0.9	16.7							0.4	16.0					0.3	39.6
PODU	FW	1.0	33.6	0.4	16.7									0.2	10.7			0.9	49.4							0.3	28.6
	SS	0.9	56.4	0.3	6.4													1.0	45.6							0.2	28.2
TURU	FW	0.7	24.5	0.7	5.6															0.3	32.8			0.4	48.6		
	SS	0.8	23.5			0.4	30.4									0.3	9.0			0.8	48.5			0.2	10.7		
TUAM	FW											0.6	12.2			0.6	30.8	0.7	48.6	0.5	12.8			0.2	27.4		
	SS	0.4	19.3			1.0	41.7	0.3	9.9									0.5	25.8			0.3	32.5	0.3	11.8		
SAAU	FW	0.6	14.5			0.4	22.9									0.4	21.1	0.5	30.0			0.5	42.6				
	SS	1.0	46.0			0.8	30.1	0.3	7.8									0.3	24.7			0.7	53.9				
PACO	FW	0.2	17.4									0.8	24.5	0.5	23.4	0.2	26.2	0.6	65.4								
	SS											0.9	34.0					0.9	50.4							0.9	17.4
POME	FW	1.0	26.5					0.9	56.8											0.4	34.8						
	SS									1.0	11.0	1.0	23.2	1.0	33.8			0.6	38.6								
SUSU	FW											0.4	10.6	1.0	58.4			0.7	62.2								
	SS									1.0	43.5	0.3	10.0	0.7	39.1			0.2	56.3								
SESU	FW			0.2	13.5	1.0	34.4	0.5	14.6											0.3	18.4	0.5	44.6	0.2	18.0		
	SS	0.9	40.0															0.8	36.3	0.8	25.6						
SIFL	FW	1.0	36.7	0.2	14.2	0.3	20.6											0.7	34.1								
	SS	1.0	68.2			0.5	5.2	0.4	14.6									0.7	42.9	0.2	15.9						
MYMO	FW					0.7	28.9	0.5	20.0											0.3	27.4			0.3	32.0		
	SS	0.2	11.5			0.4	28.3									0.3	32.1			0.3	27.4			0.3	32.0		

[†] Codes of bird species listed in Table A1.1.
[‡] FW = fall-winter, SS = spring-summer.
[§] Patch-scale variables: D_Arb = density of trees, D_arb = density of shrubs, A_Arb = tree height, DBH = diameter at breast height, PA = patch area (ha), SI = shape index, FD = fractal dimension, DistLoc = linear distance (m) to nearest settlement.
[ǀ] Landscape-scale variables: PC1 = fragmentation gradient principal component, PC2 = fragmentation covariate principal component, IJI = interspersion and juxtaposition, CO = Contagion, and PR = cover type richness.

taking advantage of holes made by medium-sized woodpeckers. The existing Espinal forest is mostly secondary, where stands commonly include trees of different sizes and ages. In summary, the forest patch characteristics and historical land use, e.g., proportion of shrub cover, degradation, livestock ranching, and extraction of mature trees, may explain the lack of an observed inverse relationship between tree density and availability of nest cavities. Regarding other species like Monk Parakeet and Picui Ground Dove, preference for patches characterized by reduced tree density could facilitate the detection of potential nest predators (Peris and Aramburú 1995, Eberhard 1998).

Most species in our study did not respond to forest patch size contrary to other studies that reported a response (positive or negative) between bird abundance and patch size (Robinson et al. 1995, Estades 2001, Lindenmayer et al. 2002, Ferraz et al. 2007). This suggests ecological processes manifested at certain spatial scales may be of greater importance. For example, patch size response may be influenced by species-specific characteristics such as life history strategies or attributes of the landscape. Similarly, abundant species may be present in small patches (MacNally et al. 2000), other species may increase in abundance in proportion with patch size (Vickery et al. 1994, Johnson and Igl 2001), while others may exhibit no definite pattern (Andrén 1994, Estades and Temple 1999). In our study, the relatively weak influence of patch size could be related to the absence of clear statistical differences between landscapes. However, this relationship was identified, i.e., PC1, at the landscape scale, suggesting large tracts of continuous forest in mosaic 1 could still support vulnerable bird species or those sensitive to fragmentation. Conversely, these species were not abundant in landscapes characterized by relatively small forest patches surrounded by widespread agricultural development. These patterns suggest ecological thresholds, i.e., response, may exist for species requiring particular forest habitat conditions (Luck 2005, Betts et al. 2010), such as the Narrow-billed Woodcreeper, Scimitar-billed Woodcreeper, or Brown Cacholote.

Patch shape complexity was consistently important, a result similar to other published reports regarding its relationship to bird abundance (Hawrot and Niemi 1996, Magrach et al. 2011). Simpler patch shapes in our study area favored cavity nesting birds like Woodcreepers and species like Red-crested Cardinal and Suiriri Flycatcher. Patch shape is determined by the interaction between area and perimeter, which in turn determines the amount of core habitat in a fragmented landscape (Laurance and Yensen 1991, Collinge 1996). We did not quantify core area, given the extensive information in the published literature regarding core area differences among species (Watson et al. 2004, Zurita et al. 2012). Further, edge effect relationships to bird species were not part of our study objectives. Additionally, edge was not clearly defined in the Espinal forest compared to other forested biomes of southern South America, such as the Chaco forests of Argentina (Lopez de Casenave et al. 1998, Sosa 2008, Banks-Leite et al. 2010, Zurita et al. 2012). The absence of a clear edge in Espinal forest may be related to the semixerophytic nature of these forests, dominated by plant species adapted to harsh environmental conditions typical of edges, and the influence of cattle grazing in Entre Ríos province (Cano et al. 1980, Sabattini et al. 2002).

Previous information on bird use of forest edge versus interior differed among published studies. Sosa (2008) identified Masked Gnatcatcher as a forest interior species, yet in our study this was more abundant in landscapes characterized by small forest patches with little to no core habitat. Conversely, Golden-billed Saltator was reported as exclusively associated with forest edge (Sosa 2008). However, it was less abundant in study landscapes characterized by small patches and therefore lesser forest interior area. Furthermore, Dardanelli et al. (2006) differentiated use of forest interior and edge by some of the same species in our study and reported contrasting patterns to results by Sosa (2008). These differences may be due to the fact that while these other studies were also conducted in the Espinal region, the composition of tree species differed from our study area. Weather conditions in our study region also differed from Sosa (2008). Further, forest management practices in relation to fire and extractions during the first half of the 20th century resulted in changes to vegetation structure (Dussart et al. 2011). Most importantly, spatial scale may explain the differences among our study and Sosa (2008), given the area of this previous study was 9344 ha, equivalent to just one of 18 landscapes (10,000 ha) in our study.

Landscape scale factors related to amount and spatial configuration of forest were more important than other cover types, indicating bird species in our sample responded to patterns associated to forest habitat loss and fragmentation. Although many published studies highlight the quality of the matrix when determining composition and abundance of species within patches (Laurance 1991, Gascon et al. 1999, Kotze and Samways 1999, Cook et al. 2002), our results suggested the surrounding matrix exhibited a limited influence on bird abundance. A possible explanation could be that many of the selected bird species use forest patches both for feeding and nesting, which could limit their use of the matrix. On the other hand, the movements and resource selection patterns of species using both forest patches and surrounding matrix are unknown for the Espinal, so changes in land use, i.e. soybeans one year, followed by corn, may not influence avian distribution patterns. Also, bird species that actively forage in the matrix, e.g., Picui Ground Dove, may have access to food equally provided by different land use types, resulting in weak responses to quantity and spatial arrangement of crops that characterized the matrix in our study. Finally, there may be additional variables that were not incorporated or the manner in which some of the incorporated variables were measured may have failed to capture any potential influences on the bird community.

Some species in our study, e.g., Scimitar-billed Woodcreeper, Narrow-billed Woodcreeper, Brown Cacholote, Creamy-bellied Thrush, and Red-crested Cardinal, were more abundant in landscapes dominated by closely arranged, interconnected forest patches. This may reflect the benefit of increased landscape connectivity and access to available patch resources (Andrade and Marini 2001, Lees and Peres 2008). On the other hand, Picui Ground Dove, Grayish Baywing, Great Antshrike, and Saffron Finch were more abundant in landscapes characterized by greater forest fragmentation. These species are known generalists commonly found in modified agricultural landscapes. Their preference for landscapes characterized by isolated forest patches likely reflects their greater ecological plasticity in resource use (Fraser and Stutchbury 2004, Thornton et al. 2011). Our two-scale approach to assess bird responses to environmental characteristics highlighted the differential use of landscape elements by a representative sample of birds in the Espinal region. Hence, negative impacts of loss and fragmentation of native forest may not necessarily be offset by local measures alone, such as retaining large trees. Landscape scale measures describing structure, amount, and spatial configuration of forest should be considered to ensure the regional persistence of bird species. This information contributes reliable knowledge to integrate in the design of conservation measures for agricultural landscapes in the Espinal region of Argentina.

CONCLUSIONS

In the absence of land use regulations agricultural expansion will continue in the province of Entre Ríos, with increasing alteration of native forest cover, spatial configuration, and structure within patches. Our results provide useful and reliable information for the development of management and land conservation plans. As such, these may serve to provide guidance on landscape conservation design for the fragmented agroecosystems of the region. At the patch scale, retaining larger trees in forest patches will help maintain the abundance of forest species while allowing agricultural activities inside regular lots. At the landscape scale, limiting the conversion of forests to agricultural lands, avoiding further fragmentation of forest patches, and designating areas where large forest fragments are protected and maintained will benefit forest specialist species. To prevent major negative effects on biodiversity, additional conservation efforts are necessary. Some of these are currently in progress, including the National Law to protect Argentine forests. However, its effectiveness will depend on decision makers and land owners given the lack of control on land use policies. If soybean production and cattle ranching continue to expand across the Espinal forest ecosystem without land use planning, the negative effects of these activities on avian biodiversity will likely continue to increase.

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1222

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Appendix 1

Table A1.1 Bird species sampled in 45 forest patches during the austral fall-winter and spring-summer seasons of 2007 and 2008 in the province of Entre Ríos, Argentina. The code of species was determined by the first two letters of gender and the first two letters of the species.

Scientific name	Common name	Code
Columbina picui	Picui Ground Dove	COPI
Agelaioides badius	Grayish Baywing	AGBA
Drymornis bridgesii	Scimitar-billed Woodcreeper	DRBR
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	LEAN
Synallaxis frontalis	Sooty-fronted Spinetail	SYFR
Pseudoseisura lophotes	Brown Cacholote	PSLO
Taraba major	Great Antshrike	TAMA
Polioptila dumicola	Masked Gnatcatcher	PODU
Turdus rufiventris	Rufous-bellied Thrush	TURU
Turdus amaurochalinus	Creamy-bellied Thrush	TUAM
Saltator coerulescens[†]	Grayish Saltator	SACO
Saltator aurantiirostris	Golden-billed Saltator	SAAU
Paroaria coronata	Red-crested Cardinal	PACO
Poospiza melanoleuca	Black-capped Warbling Finch	POME
Suiriri	Suiriri Flycatcher	SUSU
Serpophaga subcristata	White-crested Tyranulet	SESU
Sicalis flaveola	Saffron Finch	SIFL
Myiopsitta monachus	Monk Parakeet	MYMO
Asthenes baeri[†]	Short-billed Canastero	ASBA

[†] Species that were not included in analyses due to low number of detections.

Appendix 2

Table A2.1 Producer´s and user´s accuracy for each cover type from Landsat TM image processing for 2007 and 2008.

Class Name	2007		2008	
	Producer´s Accuracy (%)	User´s Accuracy (%)	Producer´s Accuracy (%)	User´s Accuracy (%)
Water bodies	97	99	99	99
Corn	70	71	69	68
Sunflower	100	63	99	82
Soybean	75	98	76	96
Sorghum	98	69	92	61
Other crops	82	80	71	80
Introduced forest	100	68	99	82
Native forest	72	85	91	91
Flooded vegatation	64	93	71	92
Urban-bare soil	92	95	87	89

Appendix 3

A3. Description and ecological implication of native forest composition and configuration indexes used in the study as implemented in FRAGSTAT (McGarigal et al. 2012).

A3.1 Total area of native forests (FA)

$$\sum_{\mathrm{j}=1}^{a} a_{\mathrm{ij}}\ (1/10{,}000)$$

a_{ij} = patch ij area (m^2)

A3.2 Number of native forest patches (NP)

Number of patches
NP = n_i
n_i = number of patches in the landscape that belongs to the same class

A3.3 Mean patch area (PA)

$$\sum_{\mathrm{j}=1}^{\mathrm{n}} \mathrm{x}_{ij} \Big/ \mathrm{n}_{\mathrm{i}}$$

x_{ij}= all patches of the corresponding patch type
n_i = number of patches

A3.4 Edge density (ED)

$$\sum_{\mathrm{k}=1}^{\mathrm{m}} \mathrm{e}_{\mathrm{ik}}/\mathrm{A}\ \ (10{,}000)$$

e_{ik} = total length (m) of edge in landscape involving patch type (class) i
A = total landscape area (m^2)

A3.5 Shape index (SI)

$$.25\ \mathrm{p}_{\mathrm{ij}}/\sqrt{\mathrm{a}_{\mathrm{ij}}}$$

p_{ij} = perimeter (m) of patch ij
a_{ij} = area (m^2) of patch ij

A3.6 Fractal dimension index (FD)

$$2\ln(.25\ \mathrm{p}_{\mathrm{ij}})/\ln \mathrm{a}_{\mathrm{ij}}$$

p_{ij} = perimeter (m) of patch ij
a_{ij} = area (m^2) of patch ij

A3.7 Perimeter-area ratio (PARA)

$$\mathrm{p}_{\mathrm{ij}}/\mathrm{a}_{\mathrm{ij}}$$

p_{ij} = perimeter (m) of patch ij

a_{ij} = area (m^2) of patch ij

A3.8 Mean Euclidean distance to forest patches (ENN)

$$h_{ij}$$

h_{ij} = distance (m) from patch ij to the nearest neighbor patch of the same class, based on patches edge to edge distance

A3.9 Cohesion index of forest patches (COH)

$$\left[1-\sum_{j=1}^{n} p_{ij} \middle/ \sum_{j=1}^{n} p_{ij}\sqrt{a_{ij}}\right].\left[1-1/\sqrt{Z}\right]^{-1}.(100)$$

p_{ij} = patch ij perimeter (number of cells)
a_{ij} = patch ij area (number of cells)
Z = total number of cells in the landscape

A3.10 Aggregation index of forest patches (AI)

$$\left[g_{ij}/\max \rightarrow g_{ij}\right](100)$$

g_{ii} = number of like adjacencies (joins) between pixels of patch type (class) i based on the single-count method.
max-g_{ii} = maximum number of like adjacencies

Appendix 4

Table A4.1 Set of plausible models describing the relationship of within patch, patch and landscape variables with bird abundance for each season. Models are shown with their AICc values and Akaike weight (ωi). Best set of models were those having ΔAICc ≤ 2 (Burnham and Anderson 2002). ΔAICc= AICi –AICmin values. Parentheses indicate a negative relationship to bird abundance.

Species†	Season‡	Scale§	Model	AICc	Akaike weight (ωi)
COPI	FW	Patch	(-D_Arb) + (-D_arb)	117.46	0.36
			(-D_Arb)	117.71	0.32
			(-D_Arb) + FD	119.07	0.16
			(-D_Arb) + (-D_arb) + FD	119.28	0.15
		Landscape	PC1	30.52	0.37
			PC1 + Contagion	31.94	0.18
			PC1 + (-IJI)	32.29	0.15
			PC1 + PR	32.43	0.14
	SS	Patch	(-D_Arb) + (-D_arb)	114.42	0.28
			(-D_Arb) + (-D_arb) + FD	114.54	0.26
			(-D_Arb) + FD	114.69	0.24
			(-D_Arb)	115.54	0.16
		Landscape	PC1	40.33	0.27
			PC1 + (-PR)	41.67	0.14
			PC1 + PC2	41.92	0.12
			PC1 + IJI	41.93	0.12
			PC1 + (-Contagion)	42.31	0.10
AGBA	FW	Patch	(-D_Arb)	112.09	0.32
			(-D_Arb) + (-SI)	112.68	0.24
			(-D_Arb) + (-CA)	113.90	0.13
			(-D_Arb) + (-FD)	114.10	0.12
		Landscape	(-PR)	42.27	0.32
			PC2 + (-PR)	43.64	0.16
			PC1 + (-PR)	44.23	0.12
	SS	Patch	(-D_arb)	61.92	0.36
			(-D_Arb)	63.39	0.17
			(-D_Arb) + (-D_arb)	63.95	0.13
		Landscape	PC2 + (-PR)	13.54	0.20
			PC2	13.93	0.17
			PC1 + PC2	14.67	0.12
DRBR	FW	Patch	(-SI)	-47.41	0.57
			(-SI) + (-FD)	-46.11	0.3
		Landscape	(-PC1) + (-IJI)	-40.63	0.49
	SS	Patch	(-SI) + FD + D_Arb	-27.78	0.38
			D_Arb + DBH + (-A_Arb)	-27.03	0.26
			(-SI)	-26.35	0.19
		Landscape	(-PC1)	-24.19	0.19

			(-PC1) + Contagion	-24.07	0.18
			(-PC1) + (-IJI)	-23.37	0.13
			PC2 + Contagion	-23.28	0.12
			Contagion	-23.17	0.11
			(-PC1) + PC2	-22.74	0.09
LEAN	FW	Patch	D_Arb + (-SI) + (-FD)	13.95	0.39
			D_Arb + A_Arb + DBH	13.97	0.38
			D_Arb	15.88	0.15
		Landscape	(-PC1) + (-Contagion)	1.41	0.44
			(-PC1)	3.29	0.17
			(-PC1) + IJI	3.45	0.16
	SS	Patch	D_Arb + DBH	6.80	0.69
			D_Arb + (-A_Arb) + DBH	8.53	0.29
		Landscape	(-PC1) + (-Contagion)	-2.54	0.50
			(-PC1) + IJI	-0.73	0.20
SYFR	FW	Patch	FD + A_Arb	-51.00	0.77
		Landscape	PR	-23.83	0.16
			IJI	-23.62	0.14
			(-Contagion)	-22.98	0.10
			PC2	-22.81	0.10
			(-PC1) + (-Contagion)	-22.42	0.08
			PC2 + PR	-22.23	0.07
			(-PC1)	-21.92	0.06
	SS	Patch	FD + A_Arb	46.46	0.57
			A_Arb	47.82	0.29
		Landscape	(-Contagion)	12.94	0.20
			PC2	13.40	0.16
			PC2 + (-Contagion)	14.46	0.09
			PC2 + PR	14.57	0.09
			(-PC1) + (-Contagion)	14.80	0.08
PSLO	FW	Patch	(-SI)	12.52	0.49
			(-SI) + (-FD)	13.30	0.33
		Landscape	(-PC1) + (-PR)	-4.89	0.31
			(-PC1)	-4.69	0.28
	SS	Patch	D_Arb + (-SI) + (-FD)	-15.81	0.26
			D_Arb	-15.45	0.22
			D_Arb + (-A_Arb) + DBH	-15.23	0.20
			(-SI) + (-FD)	-14.66	0.15
		Landscape	(-PC1)	-13.45	0.37
			(-PC1) + (-PR)	-11.54	0.14
			(-PC1) + (-IJI)	-11.52	0.14
TAMA	FW	Patch	D_Arb + A_Arb + SI	20.25	0.52
			D_Arb + D_arb + A_Arb	22.22	0.19
		Landscape	PC2	8.95	0.21
			(-Contagion)	9.91	0.13
			PC2 + IJI	10.24	0.11

			IJI	10.31	0.11
			PC2 + (-Contagion)	10.69	0.09
	SS	Patch	D_Arb + A_Arb + SI	-75.22	0.78
		Landscape	PC2	-34.65	0.15
			PC2 + PR	-34.50	0.14
			PR	-34.15	0.12
			PC1 + (-Contagion)	-33.87	0.10
			IJI	-33.62	0.09
			(-Contagion)	-33.20	0.07
			PC1 + PC2	-33.07	0.07
			PC2 + IJI	-33.00	0.07
PODU	FW	Patch	(-D_Arb)	83.37	0.37
			(-D_Arb) + (-D_arb)	84.01	0.27
			(-D_Arb) + FD	84.43	0.22
		Landscape	PC1	12.33	0.34
			PC1 + (-PR)	12.80	0.27
			PC1 + IJI	14.19	0.13
			PC1 + PC2	14.33	0.12
	SS	Patch	(-D_Arb)	-6.24	0.61
			(-D_Arb) + D_arb	-4.21	0.22
		Landscape	PC1	-20.03	0.33
			PC1 + (-PR)	-19.17	0.21
			PC1 + PC2	-18.71	0.17
			PC1 + IJI	-18.36	0.14
			PC1 + (-Contagion)	-18.12	0.13
TURU	FW	Patch	D_arb + D_Arb	-127.47	0.56
		Landscape	PC2 + Contagion	-9.97	0.27
			Contagion	-8.87	0.16
	SS	Patch	D_Arb	-153.84	0.39
			D_Arb + A_Arb + DistLoc	-152.73	0.22
			A_Arb	-151.85	0.14
		Landscape	PC2 + Contagion	-71.88	0.23
			PC2	-71.69	0.21
			(-PC1) + PC2	-71.51	0.19
			PC2 + PR	-71.12	0.16
TUAM	FW	Patch	DistLoc	-13.30	0.34
			(-SI) + DistLoc	-12.66	0.25
			(-SI)	-12.48	0.23
		Landscape	(-PC1) + (-PC2)	-24.22	0.47
			(-PC1) + Contagion	-22.75	0.23
	SS	Patch	A_Arb + (-DBH)	-18.31	0.32
			A_Arb	-18.15	0.29
			A_Arb + D_Arb	-17.97	0.27
		Landscape	(-PC1) + (-Contagion)	-14.38	0.30
			(-PC1) + IJI	-13.11	0.16
			IJI	-12.48	0.12

SAAU	FW	Patch	D_Arb + A_Arb	63.45	0.26
			D_Arb	63.58	0.24
			DistLoc	63.58	0.24
			FD + DistLoc	64.30	0.17
		Landscape	(-PC1) + IJI	15.80	0.31
			(-PC1)	17.02	0.17
			IJI + Contagion	17.29	0.15
	SS	Patch	D_Arb + A_Arb + (-DBH)	60.85	0.32
			D_Arb + A_Arb	60.96	0.31
			D_Arb	61.64	0.22
			D_Arb + D_arb + A_Arb	62.38	0.15
		Landscape	(-PC1) + IJI	21.72	0.33
			IJI	22.25	0.25
			IJI + Contagion	23.33	0.15
PACO	FW	Patch	(-SI)	118.48	0.34
			(-SI) + (-FD) + DistLoc	119.26	0.23
			(-SI) + (-FD)	119.84	0.17
			D_Arb	120.29	0.14
		Landscape	(-PC1)	34.75	0.33
			(-PC1) + (-PR)	36.18	0.16
			(-PC1) + (-PC2)	36.29	0.15
	SS	Patch	(-SI)	43.38	0.51
		Landscape	(-PC1) + (-PR)	3.97	0.90
POME	FW	Patch	(-D_Arb) + (-DBH)	-19.70	0.91
		Landscape	(-PC2)	-16.02	0.20
			Contagion	-15.33	0.14
			(-PC2) + IJI	-14.41	0.09
			(-PR)	-14.09	0.08
			(-PC2) + (-PR)	-14.00	0.07
	SS	Patch	CA + (-SI) + FD	-33.21	0.98
		Landscape	(-PC1)	-20.01	0.25
			(-PC1) + (-PC2)	-18.77	0.14
			(-PC1) + (-PR)	-18.29	0.11
			(-PC1) + IJI	-18.23	0.10
SUSU	FW	Patch	(-FD)	-88.69	0.57
			SI + (-FD)	-87.53	0.32
		Landscape	(-PC1)	-45.33	0.32
			(-PC1) + (-PC2)	-43.52	0.13
			(-PC1) + Contagion	-43.30	0.11
			(-PC1) + PR	-43.28	0.11
	SS	Patch	CA + (-FD)	44.09	0.45
			CA + SI + (-FD)	45.00	0.28
			CA	45.12	0.27
		Landscape	(-PC1)	6.47	0.15
			PR	6.73	0.13
			PC2	7.02	0.11

			Contagion	7.09	0.11
			IJI	7.09	0.11
			(-PC1) + Contagion	8.46	0.06
SESU	FW	Patch	(-A_Arb)	15.32	0.48
			D_arb + (-A_Arb) + (-DBH)	16.90	0.22
			(-A_Arb) + (-DBH)	17.03	0.20
		Landscape	(-IJI)	-6.50	0.24
			(-PC2) + (-IJI)	-5.43	0.14
			(-PC1) + (-IJI)	-5.06	0.12
			(-IJI) + Contagion	-5.06	0.12
			(-PC2)	-4.89	0.11
			Contagion	-4.55	0.09
	SS	Patch	(-D_Arb)	-55.90	0.48
			(-D_Arb) + D_arb	-53.89	0.17
		Landscape	PC1 + PC2	-39.13	0.81
SIFL	FW	Patch	(-D_Arb)	62.28	0.37
			(-D_Arb) + (-A_Arb)	63.29	0.22
			(-D_Arb) + D_arb	63.53	0.20
			(-D_Arb) + FD	64.30	0.13
		Landscape	PC1	14.59	0.31
			PC1 + (-PR)	16.25	0.13
			PC1 + PC2	16.44	0.12
			PC1 + Contagion	16.50	0.12
	SS	Patch	(-D_Arb) + (-A_Arb) + DBH	114.85	0.38
			(-D_Arb)	115.35	0.29
			(-D_Arb) + (-D_arb)	116.45	0.17
		Landscape	PC1	39.92	0.35
			PC1 + PC2	40.81	0.22
			PC1 + PR	41.39	0.17
MYMO	FW	Patch	(-A_Arb) + DBH	161.96	0.41
			(-A_Arb)	163.55	0.19
		Landscape	Contagion	60.82	0.19
			(-PC2)	61.14	0.16
			(-IJI)	62.48	0.08
			(-PC2) + Contagion	62.72	0.07
			(-PC1) + (-PC2)	62.73	0.07
	SS	Patch	DistLoc	141.20	0.31
			(-A_Arb)	142.14	0.19
			CA	143.08	0.12
			D_Arb + (-A_Arb)	143.18	0.12
		Landscape	(-PC2)	51.74	0.17
			Contagion	51.85	0.16
			(-IJI)	52.80	0.10
			(-PC1) + (-PC2)	53.23	0.08
			(-PC2) + Contagion	53.54	0.07
			(-PC2) + PR	53.54	0.07

	(-PC1)	53.71	0.06
	(-PC2) + (-IJI)	53.72	0.06

[†] Codes of bird species listed in Table A1.1.

[‡] Seasons: FW = fall-winter, SS = spring-summer.

[§] Spatial scale: Patch-scale variables: D_Arb = density of trees, D_arb = density of shrubs, A_Arb = tree height, DBH = diameter at breast height, PA= patch area (ha), SI= Shape index, FD= fractal dimension, DistLoc= linear distance (m) to nearest settlement. Landscape spatial configuration: PC1 = fragmentation gradient principal component**,** PC2 = fragmentation covariate principal component, IJI = interspersion and juxtaposition, Contagion and PR = cover type richness.

Appendix 5

Table A5.1 Mosaic description based on patch and landscape variables during 2007 and 2008 in the province of Entre Ríos, Argentina. Values are mean ± SE in ().

Scale	Variable	Description	Mosaic I	Mosaic II	Mosaic III
Patch	Measured on the 45 patches of forest				
	D_Arb	Mean tree density (indiv/ha)	355.49 (±36.35)^{a}	451.18 (±24.73)^{a}	166.05 (±28.90)^{b}
	D_arb	Mean shrub density (indiv/ha)	528.47 (±84.21)	462.30 (±79.18)	288.77 (±46.48)
	A_Arb	Mean tree height (m)	4.44 (±0.18)^{a}	5.39 (±0.18)^{b}	4.83 (±0.22)^{ab}
	DBH	Mean diameter at breast height	15.76 (±0.92)	17.04 (±0.87)	15.94 (±0.97)
	PA	Patch area (ha)	33.73 (±7.20)	48.55(±11.75)	29.21 (±7.41)
	SI	Shape index	1.35 (±0.05)^{a}	1.45 (±0.08)^{a}	1.63 (±0.09)^{b}
	FD	Mean patch fractal dimension	1.26 (±0.01)^{a}	1.26 (±0.01)^{a}	1.29 (±0.01)^{b}
	DistLoc	Mean linear distance to nearest settlement (m)	8923.8 (±1138.33)	4869.73 (±657.08)	7104.33 (±1213.52)
Landscape (Forest class)	Measured on the 18 sub-landscapes				
	FA	Total cover of forest areas (ha)	5617.21 (±410.33)^{a}	2308.67 (±295.69)^{ab}	303.58 (±134.50)^{b}
	NP	Total number of forest patches	24.58 (±2.82)^{ab}	39.50 (±5.36)^{a}	17.33 (±5.26)^{b}
	PA	Mean area of forest patches (ha)	253.95 (±40.03)^{a}	64.36 (±12.85)^{ab}	15.12 (±4.19)^{b}
	ED	Edge density (m/ha)	53.27 (±4.02)^{a}	110.06 (±16.26)^{ab}	368.76 (±81.84)^{b}
	SI	Shape index	2.09 (±0.08)^{a}	2.18 (±0.11)^{a}	4.18 (±0.69)^{b}
	FD	Fractal dimension	1.10 (±0.01)^{a}	1.10 (±0.01)^{a}	1.16 (±0.01)^{b}
	PARA	Area-perimeter ratio	1167.49 (±343.40)	450.17 (±79.80)	664.97 (±135.34)
	ENN	Mean euclidean distance among forest patches (m)	57.83 (±7.83)^{a}	157.14 (±112.19)^{b}	833.22 (±395.73)^{b}
	COH	Forest patch cohesion	99.94 (±0.03)^{a}	99.71 (±0.05)^{a}	99.11 (±0.15)^{b}
	AI	Aggregation index	99.33 (±0.05)^{a}	98.60 (±0.23)^{ab}	93.82 (±1.92)^{b}

Landscape (all class)	Measured on the 18 sub-landscapes		2007	2008	2007	2008	2007	2008
	CO	Contagion	54.31 (±2.71)	56.91 (±2.07)[a]	52.12 (±1.22)	46.02 (±1.42)[b]	54.09 (±1.35)	44.52 (±0.54)[b]
	IJI	Interspersion and Juxtaposition	59.22 (±1.04)	67.44 (±1.82)	62.46 (±0.91)	70.59 (±20.05)	60.49 (±1.95)	67.46 (±1.04)
	PR	Class richness in landscape	10.50 (±0.22)	9.50 (±0.22)	10.50 (±0.34)	9.50 (±0.22)	9.50 (±0.43)	9.33 (±0.33)

[a] and [b] indicate statistical differences of variables between mosaics. Means with a common letter are not significantly different ($P > 0.05$) by Kruskal Wallis test.

Appendix 6

Table A6.1 Correlation matrix of forest patch scale and landscape variables. D_Arb = density of trees, D_arb = density of shrubs, A_Arb = tree height, DBH = diameter at breast height, PA= patch area (ha), SI= Shape index, FD= fractal dimension, DistLoc= linear distance (m) to nearest settlement, PC1 = fragmentation gradient principal component**,** PC2 = fragmentation covariate principal component, IJI = interspersion and juxtaposition, CO = Contagion and PR = cover type richness.

	D_Arb	D_arb	A_Arb	DBH	PA	SI	FD	DistLoc	PC1	PC2	IJI	Contagion
D_arb	0.49											
A_Arb	0.33	-0.02										
DBH	0.08	-0.28	0.67									
PA	0.03	-0.03	0.17	0.08								
SI	-0.33	-0.06	-0.03	-0.19	0.24							
FD	-0.32	-0.12	-0.20	-0.23	-0.34	0.74*						
DistLoc	0.04	0.02	-0.53	-0.27	-0.23	0.08	0.33					
PC1	-0.69	-0.45	-0.02	0.01	0.06	0.69	0.58	-0.16				
PC2	0.28	-0.03	0.79*	0.50	0.15	0.03	-0.09	-0.20	0.01			
IJI	0.32	-0.19	0.53	0.39	-0.06	-0.06	0.05	0.12	-0.11	0.57		
Contagion	0.05	0.31	-0.62	-0.46	-0.14	-0.36	-0.26	0.18	-0.47	-0.74*	-0.61	
PR	0.51	0.47	0.26	0.02	0.23	-0.09	-0.16	-0.10	-0.52	0.28	-0.25	0.15

*P=0.05