



Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico



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ABSTRACT

With accelerated land-use change throughout the tropics, an increasing proportion of global biodiversity is located in human-modified landscapes. Understanding the relative effects of landscape composition and configuration on biodiversity is needed to design effective conservation strategies. Yet this topic is poorly understood because most studies have been performed at the patch scale, and do not assess the impact of landscape structure on species. Using a multi-model inference approach, we assessed the relative effect of landscape composition (i.e. percentage of forest cover and matrix composition) and landscape configuration (i.e. number of forest patches and forest edge density) on α - and β -diversity of birds in 17 forest fragments and three areas of continuous forest within the Lacandona rainforest, Mexico. We tested these impacts at two spatial scales (100 and 500 ha) for forest specialist and generalist birds. In general, forest specialist birds showed stronger responses to landscape characteristics than generalist species, particularly to variations in landscape composition at the 100-ha scale. The loss of forest cover represented the main threat to forest specialist birds, with a negative impact on α -diversity that was consistent across the two spatial scales. In contrast, at the two spatial scales generalist birds seemed to be favored by forest loss, as α -diversity of these birds increased in landscapes with lower forest cover and higher number of forest patches. If current deforestation rates continue, several forest specialists are likely to disappear. Future conservation and management initiatives should therefore prevent deforestation in this biodiversity-rich but vanishing tropical forest ecosystem.

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1. Introduction

Continuous rainforests are being rapidly converted to human-modified tropical landscapes (HMTLs), largely due to accelerated human population growth and increasing demands for agricultural lands and forest products (Laurance et al., 2014). These landscapes are highly heterogeneous, showing different composition and spatial configuration, where composition refers to the types and proportions of different forms of land covers, and configuration refers to the spatial arrangement of a given land use/land cover class (sensu Dunning et al., 1992). Both landscape composition and configuration defines the heterogeneity or structure of a landscape, and can have different impacts on biodiversity (Fahrig,

2003; Fahrig et al., 2011; Tschardt et al., 2012; Newbold et al., 2014). Nevertheless, the available information on this topic is very scarce as most studies in HMTLs have been performed at the patch scale, and do not assess, nor control for, the independent effects that landscape composition and configuration may have on biodiversity (Fahrig, 2003). Also, the majority of existing landscape-scale studies are focused on temperate ecosystems (McGarigal and Cushman, 2002). It is thus necessary to adopt a landscape perspective that distinguishes between composition and configuration in tropical ecosystems, to obtain a better understanding of species' responses to land-use changes in HMTLs, and improve management and conservation strategies in the tropics (Gardner et al., 2009; Melo et al., 2013).

Studies from temperate forests evaluating the independent effects of landscape composition and configuration have usually found that landscape configuration (e.g. number or density of

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forest patches) shows a variable and weaker effect on biodiversity than landscape composition (e.g. habitat amount) (Trzcinski et al., 1999; Fahrig, 2003; Smith et al., 2011). In fact, fragmentation per se (i.e. the breaking apart of habitat after controlling for habitat loss; sensu Fahrig, 2003) can have negative, positive, or neutral effects on different taxa (Fahrig, 2003; Betts et al., 2006; Ethier and Fahrig, 2011). The negative effects can be related to the loss of landscape connectivity and the increase in forest edge (Murcia, 1995; Laurance et al., 2002). Nevertheless, by increasing the number of patches, fragmentation can promote the creation of subpopulations, favoring metapopulation dynamics and species persistence in more fragmented landscapes (Hanski, 1999). Other positive effects of fragmentation per se reviewed by Fahrig (2003) include: (1) increasing access to resources in forest edges, (2) reducing inter-patch isolation distances with increasing fragmentation per se; and (3) improving access from home patches to resources located in other neighboring patches, as indicated in the landscape complementation and supplementation hypotheses (Dunning et al., 1992).

In forested landscapes, variations in species responses to forest fragmentation and inter-patch isolation may be related to differences in the amount of old-growth forest cover in the landscape (Villard and Metzger, 2014) and to differences in matrix composition (Fahrig et al., 2011). Evidence indicates that the effect of forest fragmentation may be higher in landscapes with lower (Trzcinski et al., 1999) or intermediate forest cover (Villard and Metzger, 2014). At the same time, landscapes with heterogeneous matrices, such as those with live fences, isolated trees, secondary forests, and different types of land covers, can maintain more resources (Dunning et al., 1992; Fahrig et al., 2011) and higher landscape connectivity (Antongiovanni and Metzger, 2005; Fahrig, 2007), thus supporting more species than landscapes with homogeneous matrices (see the “landscape insurance hypothesis”; Tschardt et al., 2012). For example, secondary forests are expected to contain resources for both forest specialist and habitat generalist birds (Blake and Loiselle, 2001), and also improve landscape connectivity for forest-specialist species (Stouffer and Bierregard, 1995; Pinotti et al., 2012). In contrast, open-habitat matrices can inhibit birds' dispersal movements in HMTLs (Castellón and Sieving, 2006; Ibarra-Macias et al., 2011).

Changes in landscape composition and configuration not only alter patterns of local diversity (α), but also the composition and structure of remaining assemblages, potentially altering the species turnover (β -diversity) across multiple spatial scales (Flohre et al., 2011; Karp et al., 2012; Arroyo-Rodríguez et al., 2013; Püttker et al., 2014). For example, both increases (i.e. biotic differentiation) and declines (i.e. biotic homogenization) of β -diversity have been reported in HMTLs (Arroyo-Rodríguez et al., 2013). However, the relative impact of landscape composition and configuration on β -diversity remains poorly understood, particularly in the tropics (but see Karp et al., 2012).

Here we examined the relative effects of landscape composition and configuration on α - and β -diversity of birds within old-growth forest in a fragmented biodiversity hotspot – the Lacandona rainforest, Mexico. As landscape composition we considered the percentage of old-growth forest cover in the landscape and the percentage of secondary forest cover in the matrix. As measures of landscape configuration we included the number of old-growth forest patches and forest edge density. Since the responses of species to landscape composition and configuration can be scale-dependent (Smith et al., 2011; Thornton et al., 2011; Garmendia et al., 2013; San-José et al., 2014), these landscape metrics were measured at two spatial scales, within 100-ha and 500-ha landscapes. Also, as the impact of landscape change on species may vary according to the habitat specificity of species (Fahrig, 1998; Lindell et al., 2004; Pardini et al., 2010; Newbold et al., 2014), we

separately assessed the response of forest interior specialist (those that use forest as the primary habitat) and habitat generalist species (those that use resources from different land covers and forest strata in HMTLs).

Based on the hypotheses and empirical evidence described above, we predicted that both α - and β -diversity will have stronger associations with landscape composition, than with landscape configuration, particularly when considering forest specialist species, which will be strongly and positively associated with the percentage of old-growth forest cover in the landscape. It has been reported that forest edge density in the landscape can have both positive and negative effects on biodiversity, depending on the vulnerability of the species to forest edge effects (reviewed by Ewers and Didham, 2006). Thus, we predicted that forest interior specialist species will have a negative association with forest edge density, whereas forest generalist species would be positively related to this factor because of increasing access to resources, in both forest edges and the neighboring matrix. Finally, regarding the composition of the landscape matrix, secondary forests are expected to contain more resources and refuges for both specialist and generalist birds than other covers of the matrix (Stouffer and Bierregard 1995; Pardini et al., 2005; Banks-Leite et al., 2010); thus, we predicted that the diversity of birds will increase in patches surrounded by a matrix dominated by secondary forests.

This is a timely study for the conservation of birds, given that: (1) landscape-scale studies on tropical birds are very scarce (but see Cerezo et al., 2010; Kennedy et al., 2011); (2) the Lacandona region is one of the biologically richest Mexican ecosystems (González-García, 1993; Medellín, 1994); and (3) the region is experiencing a very high annual deforestation rate (annual rate of 2.1% between 1990 and 2010; Courtier et al., 2012), but to our knowledge, no study to date has evaluated the impact of landscape spatial changes on bird community in this vanishing biodiversity hotspot.

2. Materials and methods

2.1. Study area

The Lacandona region is located in the southern part of Chiapas, Mexico (100–1500 m a.s.l.; Fig. 1), and represents the westernmost part of the Mayan forest, which extends through Guatemala to the Belize Mayan Mountains, and north to the middle portion of the Yucatan Peninsula. With an extent of 13,000 km², this region represents one of the largest areas of tropical rainforest in Mexico, and a priority area for biodiversity conservation in Mesoamerica. Yet it has been strongly deforested during the last 40 years, owing to national policies that promoted agroforestry, agriculture, and cattle ranching. This was particularly evident in the Marqués de Comillas region (MCR) (Martínez, 2003; Courtier et al., 2012), which is located in the southeastern border of the Montes Azules Biosphere Reserve (MABR; Fig. 1). The climate is hot and humid, with annual precipitation averaging 2500–3500 mm, and average monthly temperatures of 24–26 °C. The study was conducted in two adjacent lowland areas (100–200 m a.s.l.) with similar soil and weather conditions, thus avoiding confounding factors related to altitude, weather and soil. These areas, the continuous forest of MABR and the fragmented forest of MCR, are separated by the Lacantún River (Fig. 1).

2.2. Study landscapes

Following McGarigal and Cushman (2002), we adopted a patch-landscape approach, in which response variables are evaluated within old-growth forest patches (forest patches hereafter) and

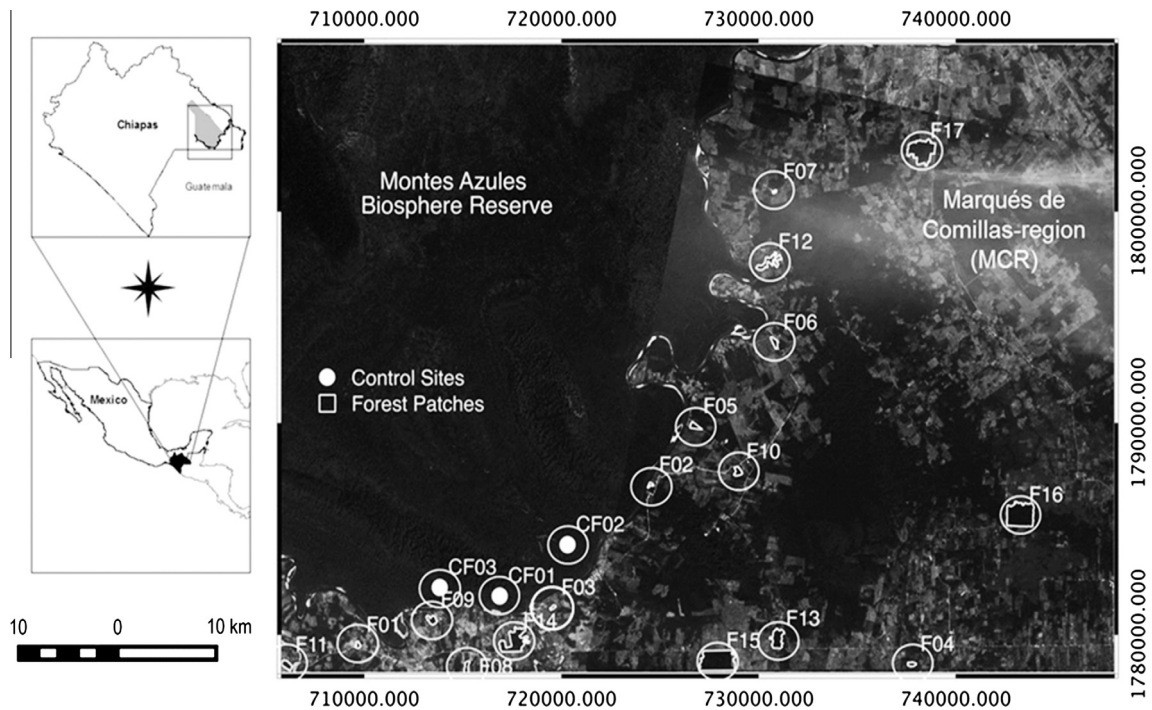


Fig. 1. Location of 17 forest patches in the Marqués de Comillas region (MCR) and three reference areas within the Montes Azules Biosphere reserve (MABR) in the Lacandona rainforest, southeastern Mexico. The 500-ha buffers surrounding each sampling site is also indicated (the spatial structure of such buffers is indicated in Fig. 2).

landscape variables are measured within a specified radius from the center of these patches. In particular, we sampled 20 sites: 17 forest patches in MCR, ranging from 3 to 92 ha, and separated from each other by at least 2 km, and three areas (100 ha each) of continuous forest in MABR separated from each other by at least 4 km and located at least 1 km from the forest edge (Fig. 1). With recent SPOT 5 satellite images (March 2011) and the “region growing” algorithm of the GIS SPRING program (Camara et al., 1996) we first made a supervised classification considering six land cover types: old-growth forests, secondary forests, arboreal crops (i.e. palm and rubber plantations), shrub crop (i.e. corn, chili and bean plantations), cattle pastures, and human settlements. Then, based on field observations in 152 sampling points distributed throughout the region, we found that overall classification accuracy was 77%. We finally used the GIS GRASS program (GRASS, 2011) to characterize the spatial configuration of the landscapes surrounding each site (i.e. forest patches and reference areas) at two spatial scales: within a 100-ha buffer and within a 500-ha buffer from the center of each sampling site (100- and 500-ha landscapes, hereafter; Figs. 1 and 2; also see online Appendix Table A1). We selected these buffer sizes because they are large enough to include the home range of several populations of birds (see Odum and Kuenzler, 1955; Schoener, 1968, and reference therein), as well as large variation in the explanatory variables (Table A1).

2.3. Bird surveys

Birds were sampled using unlimited radius point counts (Bibby et al., 2000). All points were located inside the forest, that is, forest patches in MCR and reference areas within MABR. Each site (patch and reference area) was sampled three times, once per month, between May and August 2012 (wet season), following a randomly selected order. Point counts were distributed by dividing each site in three sections, and during each visit we sampled a different section. During each visit, point counts were separated 200 m from each other to increase independency (Hutto et al., 1986). The number of point counts was proportional to the size of the patches,

with three point counts sampled in patches of <10 ha, 6 points in patches of 10–30 ha, 9 points in patches of 30–50 ha, and 15 points in patches of >50 ha. The number of point counts conducted in our reference areas (MABR) varied from 21 to 30, because of variations in weather conditions during our sampling dates. The total points surveyed were 130 in patches and 72 in continuous forest. In each point count we recorded all birds seen or heard during a 15 min period. We only considered birds that were perched on trees, on the floor, feeding or using other resources of the forest. We ignored birds that fly by our point counts. Surveys began at sunrise (5.30 am) and finished at 10.30 am. Data in all point counts was collected by the same observer (E.C.).

Based on Stotz et al. (1996), the species were classified in two groups: (1) forest interior specialists (species inhabiting forest interior and that are rarely found in other habitat types); and (2) habitat generalists (species that use a variety of habitats including forest interior, secondary forests, forest edges and open areas). We excluded migratory birds, aquatic birds, raptors, or nocturnal birds, as our point count sampling method was not designed to sample effectively all these groups. Due to identification problems, species from the Troglodytidae family were also excluded from the analysis.

2.4. Response variables

Our response variables were mean α -diversity per patch and β -diversity within patches. We first evaluated the accuracy of bird inventories, using the coverage estimator for infrequent species recommended by Chao and Jost (2012) with the SPADE program (Chao and Shen, 2010):

$$\hat{C}_{infreq} = 1 - \frac{Q_1}{\sum_{i=1}^k iQ_i} \left[\frac{(t-1)Q_1}{(t-1)Q_1 + 2Q_2} \right]$$

where Q_k is the number of species that are observed in exactly k point counts ($k = 1, 2, \dots, t$), based on presence/absence data. Thus,

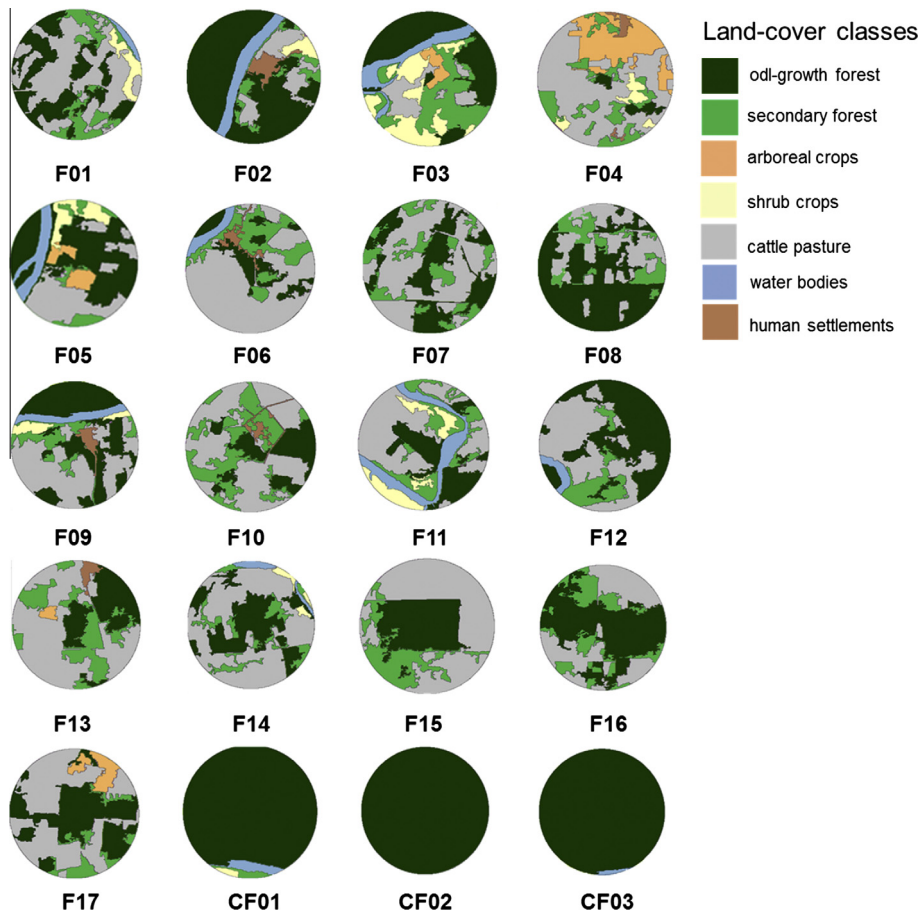


Fig. 2. Spatial structure of the 500-ha landscapes studied in the Lacandona ranforest, Mexico. Numbers correspond to those showed in Fig. 1 and Table A1.

Q_1 and Q_2 are the number of species observed in one and two point counts, respectively.

Because sampling coverage was highly variable among sites (Table A1), we used the average number of species per sample point as the response variable (mean α -diversity), which was not related to the number of count points within the sites ($R^2 = 0.02$, $p = 0.53$), being thus independent of sampling effort. β -diversity within each site was first calculated using a multiplicative partition (Jost, 2007; Whittaker, 1960), i.e. $\beta = \gamma/\alpha$, where α refers to mean α -diversity per count point, and γ refers to the total number of species sampled in each site. Nevertheless, because this measure was significantly correlated with sampling effort, we used the minimum number of points ($n = 3$) per site. In particular, in sites with >3 points, we randomly selected a sampling point within each site, and we then selected the two nearest points to avoid the bias associated with differences in inter-point distance. Thus, β -diversity was finally estimated considering γ -diversity and mean α -diversity within these 3 points.

2.5. Predictor variables

For all 100- and 500-ha landscapes we measured metrics of landscape composition and configuration that can be of key relevance for birds (Villard et al., 1999; Trzcinski et al., 1999; Cerezo et al., 2010; Smith et al., 2011) and other organisms (reviewed by Ewers and Didham, 2006). In particular, composition metrics were the percentage of old-growth forest cover in the landscape, and the percentage of the matrix covered by secondary forests. The later metric was selected because secondary forests are very common in the region (Table A1), and this land cover is the most

similar to the original vegetation in terms of composition and structure, thus representing a good indicator of matrix permeability to movements of birds, as well as of resource availability within the matrix, particularly for forest specialist species. Also, the percentage of the matrix covered by secondary forests was not correlated with the percentage of the matrix covered by other land covers in the matrix ($p > 0.13$ in all cases and for both spatial scales), thus indicating that this metric was independent of the composition of other land cover classes in the matrix. Configuration metrics included the number of old-growth forest patches in the landscape and forest edge density, which was measured as the length of all old-growth forest borders divided by the total area of the landscape (expressed as m/ha). Other aspects of landscape configuration, such as forest patch aggregation and connectivity were not explicitly addressed. Reference areas were considered as having 100% forest cover, zero forest edge density, and zero percentage of secondary forest in the matrix (Table A1).

2.6. Data analyses

To identify the landscape attributes with the strongest influence on α - and β -diversity of forest specialists and generalists we used generalized linear models (Crawley, 2007). We fixed a Gaussian distribution after verifying that α - and β -diversity showed a Normal distribution (Shapiro–Wilk test). To avoid multi-collinearity problems between the predictor variables in multivariate models, we estimated the variance inflation factor (VIF) of each predictor using the *car* package for R version 3.0.1 (R Core Team 2013). Generally, a VIF > 4 indicates possible collinearity, and a VIF > 10 indicates severe collinearity (Neter et al., 1996). Our analysis

indicated a possible collinearity between factors measured at different scales. Thus, we performed two independent analyses: one for assessing the effect of the 100-ha landscape metrics and one for the 500-ha landscape metrics. Because the three reference areas showed the same values for all landscape metrics (Table A1), we merged the response variables from these three reference areas into one single value by considering mean α - and β -diversity per reference area. We therefore included one single reference site in the regression models, thus avoiding pseudoreplication problems.

We used a multi-model inference approach to identify the subset of models with the most empirical support, from a total of 16 possible models (Burnham and Anderson, 2002). We ranked the models from the best to the worst based on the Akaike's information criterion corrected for small samples (AICc). The set of models with a difference in AICc (Δ AICc) < 2 from the top model were considered to have equivalently strong empirical support and similar plausibility (Burnham and Anderson, 2002). To evaluate the importance of each predictor and produce model-averaged parameter estimates, we used Akaike weights (w_i), which represent the probability that a particular model is selected as the best fitting model if the data are collected again under identical circumstances (Whittingham et al., 2005). This model can be therefore considered as the best model for a particular dataset. Thus, we summed w_i of ranked models until the total was >0.95 (Whittingham et al., 2005). The set of models for which $\sum w_i$ was 0.95 represents the models for which we have 95% confidence that the set contains the best approximating model out of our 16 candidate models (Burnham and Anderson, 2002; Whittingham et al., 2005). The relative importance of each predictor was assessed based on the sum of Akaike weights ($\sum w_i$) of each candidate model in which such predictor appeared (Burnham and Anderson, 2002). All models were built using the package *glmulti* for R version 3.0.1 (Calcagno and Mazancourt, 2010). Following Crawley (2007), the goodness-of-fit of the models was estimated as: (explained deviance by the complete model \times 100)/explained deviance by the null model.

3. Results

We recorded 84 bird species from 25 families (Table A2). Nine species (11%) were ubiquitous, occurring in all reference sites and in >80% of the patches. In contrast, 11 species (12%) were only recorded in reference sites, and 16 species (19%) were recorded exclusively in forest patches. Overall, 20 species (24% of all species recorded) were forest specialist, and 64 (71%) were generalist species (Table A2).

3.1. Species response to changes in landscape composition and configuration

Our results indicate that a model-averaging approach was appropriate because for most cases, the best model received limited support (i.e. low Akaike weights) relative to alternative models (Table A3). In general, the diversity of forest specialist species had a stronger association with the landscape metrics (10–54% of explained deviance; Fig. 3) than the diversity of forest generalist birds, in which the models explained \leq 23% of total deviance (Fig. 4). Also, in both groups of species the associations were stronger for α -diversity (10–54% of explained deviance) than for β -diversity (10–24% of explained deviance).

For the forest specialist group, the strongest association between species diversity and landscape metrics was found for α -diversity at the 100-ha landscape scale (54% of explained deviance, Fig. 3a and b). In particular, α -diversity of forest specialists was positively associated with old-growth forest cover and

negatively related to the percentage of secondary forest cover (Fig. 3b). These relationships also hold true at the 500-ha scale (Fig. 3c and d), suggesting that these metrics are the most important landscape drivers of α -diversity of specialist birds. Interestingly, at both scales, α -diversity of forest specialists was also positively related to forest edge density, but the sum of Akaike weights was notably low (Fig. 3a and c). The effect of the number of forest patches on α -diversity was scale dependent, changing from positive at the 100-ha scale (Fig. 3b) to negative at the 500-ha scale (Fig. 3d). Surprisingly, β -diversity for this group of birds was explained mainly by a positive relation with forest edge density at both scales (Fig. 2e–h). Again, at the smaller scale there was more deviance explained (24% of explained deviance in 100-ha landscape versus 10% in 500-ha ones).

Regarding the forest generalist-species group, α -diversity increased principally with a decrease of old-growth forest and secondary forest cover, and an increase in the number of forest patches in 100-ha landscapes (Fig. 4a and b). Yet none of these factors showed a strong association with α -diversity at the 500-ha scale, as indicated by the very low Akaike weights (Fig. 4c). For β -diversity, of which only 12% of the deviance was explained at both scales, the only landscape metric included in the best models was forest cover (Fig. 3e and g), showing a negative relation with forest generalists' β -diversity (Fig. 3f and h).

4. Discussion

Our results show that landscape composition and configuration affect the diversity of rainforest birds in the Lacandona region, Mexico, adding valuable information on the drivers of species diversity in HMTLs. Several of our findings can be highlighted. First, as predicted, and consistent with previous studies in temperate areas (e.g. Fahrig, 1998, 2003; Smith et al., 2011), old-growth forest cover showed the strongest association with the diversity of forest specialist species, with a positive effect on α -diversity at both spatial scales. Second, and contrary to our expectations, forest edge density was positively related to the diversity of forest specialist species, whereas the percentage of secondary forest in the matrix tended to be negatively related to α -diversity of both forest specialist and generalist species. Third, as expected (Fahrig, 1998; Pardini et al., 2010; Newbold et al., 2014), the strength of all associations was higher for forest specialist than for habitat generalist species. Nevertheless, within both groups of birds, α -diversity was more strongly associated with landscape spatial changes than was β -diversity. Finally, in general, species diversity was more strongly associated with landscape metrics measured at the 100-ha scale than at 500-ha scale.

4.1. Species' response to landscape changes

Bird α -diversity was positively and more strongly related to variations in landscape forest cover than to variations in edge density and number of forest patches, particularly when considering forest specialist species. This result is not surprising (see Fahrig, 2003), as this ecological group is expected to be more vulnerable than the generalist group to changes in the amount of habitat available for them (Fahrig, 1998; Gillies and St. Clair, 2010; Aben et al., 2010; Newbold et al., 2014). In particular, habitat heterogeneity and resource availability is expected to increase with forest cover (Báldi, 2008; Zanette et al., 2000), thus contributing to maintain more species, particularly those that are dependent on forest interior areas (Lindell et al., 2004). Also, landscapes with higher forest cover can maintain larger populations, reducing the probability of extinction that results from demographic and environmental stochasticity (Hanski, 1999;

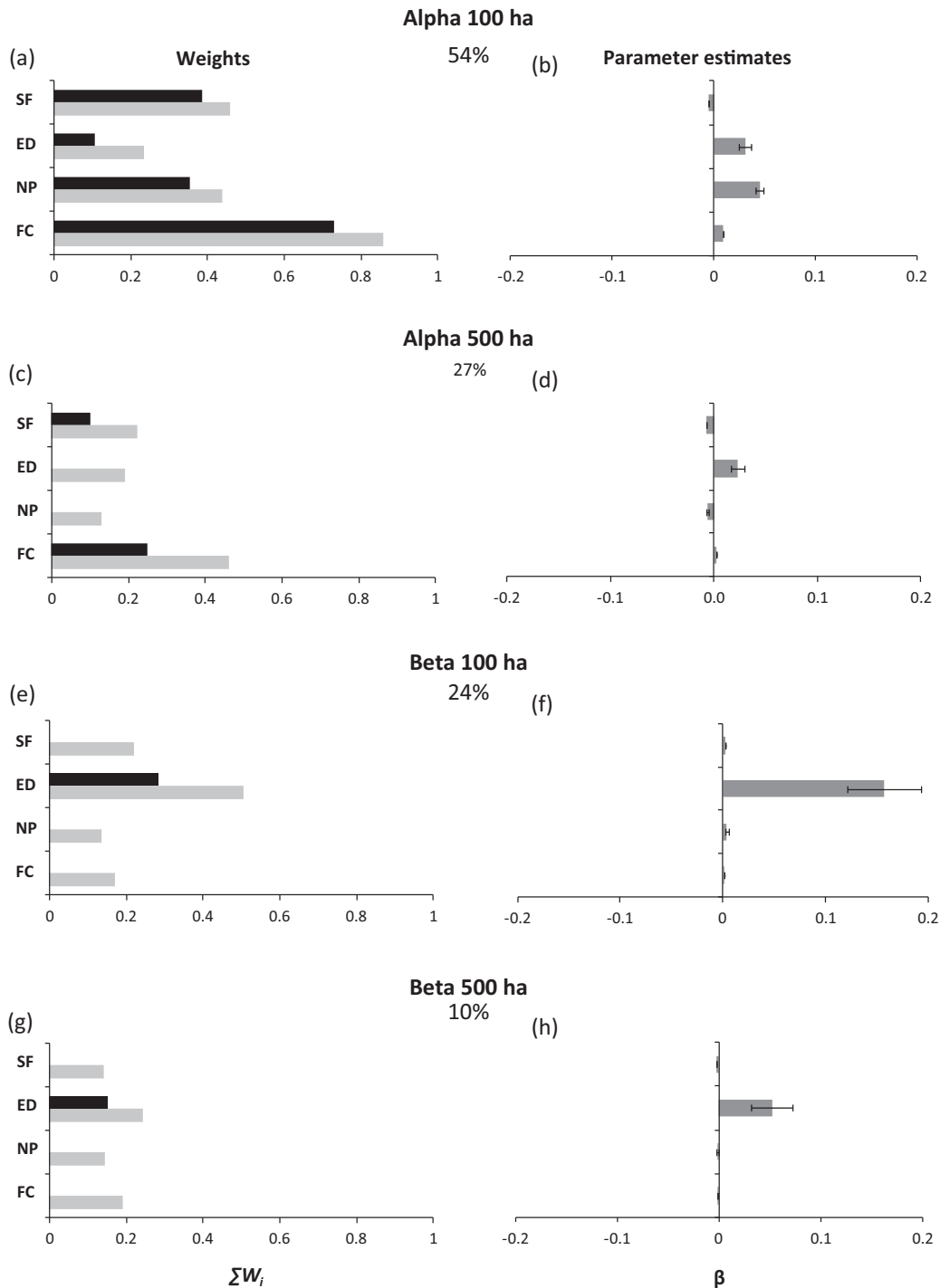


Fig. 3. Predictor variables included in the $\Delta AIC_c < 2$ set of models (black bars) and 95% set of models (gray bars) for α - and β -diversity of forest specialist birds in the Lacandona rainforest, Mexico. The importance of each variable is shown by the sum of Akaike weights (panels in the left side). In the right side, panels indicate the values of model-averaged parameter estimates (β) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference. We indicate separately the results considering two spatial scales, i.e. within 100-ha and 500-ha landscapes. The sign (\pm) of parameter estimates represent the effect (positive or negative) of each predictor on each response variable. We also indicate the percentage of explained deviance within each case. Predictors: SF (percentage of secondary forests in the matrix), ED (forest edge density), NP (number of forest patches), and FC (landscape forest cover).

Fischer and Lindenmayer, 2007). Nevertheless, because habitat generalist birds use resources not only from old-growth forests, but from other land covers in the matrix (Graham, 2001; Lindell et al., 2004), our findings indicate that their α -diversity can be negatively related to landscape forest cover, most probably because the increment in forest cover limits the availability of resources present in the matrix.

As predicted both α - and β -diversity were weakly associated with landscape configuration (i.e. edge density and number of forest patches), indicating that bird assemblages depend more strongly on differences in landscape composition, than on differences in landscape configuration (Fahrig, 2003). This suggests that the proposed difference between tropical and temperate systems may not be true. In particular, Fahrig (2003) proposes that in the

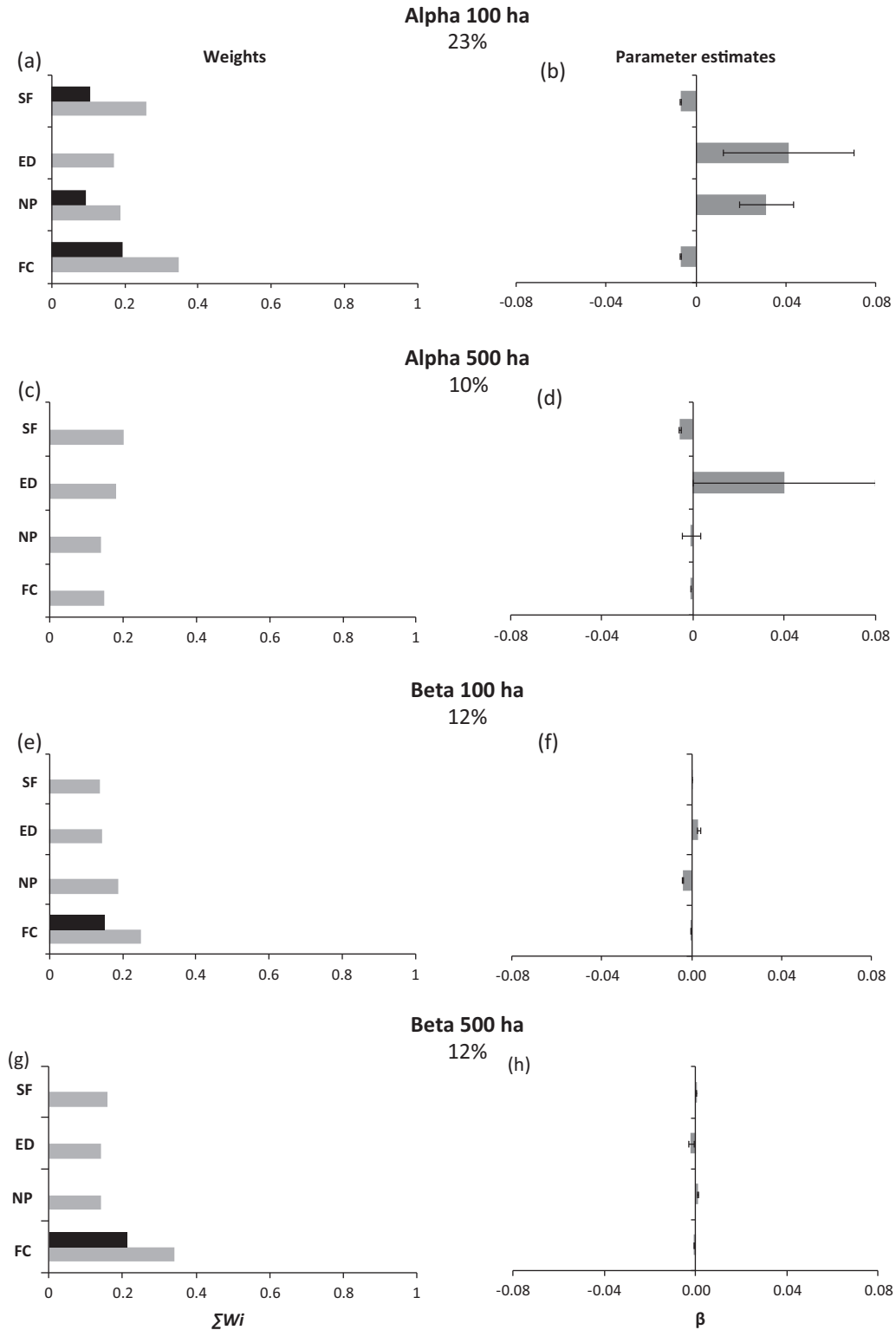


Fig. 4. Predictor variables included in the $\Delta AICc < 2$ set of models (black bars) and 95% set of models (gray bars) for α - and β -diversity of habitat generalist birds. The sum of Akaike weights (panels in the left side) indicates the importance of each variable. In the right side, panels indicate the values of model-averaged parameter estimates (β) and unconditional variance (UV) of information-theoretic-based model selection and multimodel inference. We indicate separately the results considering two spatial scales, i.e. within 100-ha and 500-ha landscapes. The sign (\pm) of parameter estimates represent the effect (positive or negative) of each predictor on each response variable. We also indicate the percentage of explained deviance within each case. Predictors: SF (percentage of secondary forests in the matrix), ED (forest edge density), NP (number of forest patches), and FC (landscape forest cover).

tropics habitat fragmentation per se (i.e. controlling for habitat loss) could have a negative effect on species diversity, as fragmentation per se results in smaller forest patches and higher forest

edge in the landscape, and tropical species usually respond negatively to these habitat spatial patterns (e.g. Laurance et al., 2002; Lindell et al., 2007). Yet we found that, in agreement with Smith

et al. (2011), the impact of forest loss was consistent across several spatial scales, whereas the impact of the number of old-growth forest patches was weak and varied across scales. This can be related to the fact that the remaining forest cover is relatively high in the region (>40% of forest cover), which means that the remaining forest patches tend to be large, presenting a high landscape connectivity, thus facilitating inter-patch animal movements (see Ewers and Didham, 2006; Fischer and Lindenmayer, 2007; Pardini et al., 2010; Villard and Metzger, 2014).

Contrary to our expectations, α -diversity of both forest specialist and generalist birds was negatively related to the percentage of secondary forests in the matrix. Both specialist and generalist birds have been observed using resources from this type of forests (Lindell et al., 2004; Gillies and St. Clair, 2010). However, there is evidence that species richness and composition in secondary forest is different from that in primary forest (Banks-Leite et al., 2010; Newbold et al., 2014), and some studies show that the ability of bird species to use secondary habitats in the tropics does not reduce their risk of becoming locally extinct as a result of deforestation (Harris and Pimm, 2004). In fact, secondary forest could be acting as ecological traps for some birds, by acting as a low-quality habitat that birds prefer over high-quality habitats (e.g. because of the very high productivity of secondary forests; Chazdon, 2014) but in which they have lower fitness (e.g. because they are exposed to higher predation pressures and competition for food resources, or present lower nesting success; see Battin, 2004). This could help to explain the negative relationship between α -diversity of both groups of birds and secondary forest in the matrix, but further studies are required to demonstrate if reproductive success is lower in secondary forests or if birds suffer higher predation pressures in this land cover type.

Forest edge density showed the weakest impact on bird diversity, but most associations with this factor tended to be positive. In fact, this factor was included in the best subset of models for α - and β -diversity of forest specialist birds at the 100-ha scale, and for β -diversity at the 500-ha scale (with a positive effect in all cases). We expected a negative impact of forest edge density because this factor is related to negative edge effects (see Lindell et al., 2007). However, forest edge density is also related to patch shape complexity, which is known to increase the probability of patch colonization, thus increasing the interchange of species and individuals in patches with more complex shapes (Ewers and Didham, 2006). This can explain why α - and β -diversity within sites increased in landscapes with higher forest edge density.

Interestingly, α -diversity was more strongly associated with landscape composition and configuration than β -diversity among sampling points (i.e. within sites). Because of dispersal limitation and variations in environmental conditions, β -diversity usually increases with the isolation distance among sampling areas (Hubbell, 2001; Karp et al., 2012; Arroyo-Rodríguez et al., 2013). Nevertheless, in our study sites the composition and structure of vegetation did not differ significantly among forest patches (Hernández-Ruedas et al., 2014), and β -diversity was estimated through points located close to each other, with inter-point distances remaining almost constant across sites. This can help to explain why the associations between the landscape predictors and β -diversity were weaker than the associations with α -diversity.

4.2. Conclusions and conservation implications

Our findings support the idea that a multi-scale analysis is required to accurately assess the impact of landscape structure on species' responses (Cerezo et al., 2010; Smith et al., 2011; Thornton et al., 2011; Fahrig, 2013), as in our study, bird diversity was more strongly influenced by local-scale landscape patterns

(i.e. by landscape metrics measured at the 100-ha than landscape metrics at the 500-ha). This can be associated with the fact that species diversity was evaluated at the patch level, and our samples were probably more representative of the 100-ha landscapes than of the 500-ha landscapes. Yet the negative impact of forest cover loss on α -diversity of specialist birds was consistent across the two spatial scales, indicating that habitat loss is an important threat to forest specialist birds in fragmented landscapes (Fahrig, 1998; Villard et al., 1999; Castellón and Sieving, 2006; Stouffer et al., 2006; Smith et al., 2011; Newbold et al., 2014). Therefore, if current land-use changes continue in the region (see Courtier et al., 2012), it is highly probable that the number of forest-dependent species will decline in the near future (Karp et al., 2012). This process could alter key ecological relationships among birds and their environment (e.g. plant pollination, seed dispersal, seed predation, pest control; Breitbach et al., 2010; Anderson et al., 2011), potentially threatening the maintenance of ecosystem integrity.

In contrast to forest specialists, however, habitat generalists seems to be favored by deforestation, as α -diversity of this group of birds was negatively related to forest cover and positively related to the number of forest patches. It is well known that species that are able to use resources from forest edges and other elements of the anthropogenic matrix, not only have a lower probability of extinction in forest patches, but they tend to be favored by deforestation (Bierregaard et al., 1992; Stouffer and Bierregaard, 1995; Laurance et al., 2002; Lindell et al., 2004; San-José et al., 2014).

Such positive effect of deforestation on generalist birds is however expected to be higher in moderately managed than in severely deforested landscapes (e.g. Melo et al., 2013). In this sense, we worked in a region in which: (1) deforestation is a relatively recent event (<40 years ago); (2) the remaining forest cover is relatively high (approximately 40%); and (3) the matrix that surrounds the forest patches is very heterogeneous. Under this landscape scenario we can expect landscape connectivity and resource availability to still be very high, thus contributing to the maintenance of their original fauna (Garmendia et al., 2013; San-José et al., 2014; Hernández-Ordóñez et al., 2014) and flora (Hernández-Ruedas et al., 2014). Yet the future of birds in this region is uncertain, as there is an increasing support for the production of oil palm (*Elaeis guineensis*) plantations (see the 'Trópico Húmedo' project; SAGARPA, 2013), and many bird species are unable to adapt to conversion of forest to oil palm plantations (e.g. Koh and Wilcove, 2008). Therefore, future conservation and management initiatives in the region should consider the key relevance of preventing further deforestation, to maintain at least the current levels of forest cover. This will help to maintain landscape connectivity and resources that can be of key relevance for the conservation of birds in this biodiversity hotspot.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.01.014>.

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