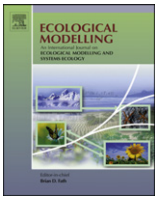
Ecological Modelling 221 (2010) 512–526

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Landscape-level impact of tropical forest loss and fragmentation on bird occurrence in eastern Guatemala

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ARTICLE INFO

Article history:
Received 29 August 2008
Received in revised form 19 October 2009
Accepted 30 October 2009
Available online 4 December 2009

Keywords:
Habitat loss
Habitat fragmentation
Landscape coherence
Scale
Autologistic regression
AIC

ABSTRACT

Tropical forest destruction and fragmentation of habitat patches may reduce population persistence at the landscape level. Given the complex nature of simultaneously evaluating the effects of these factors on biotic populations, statistical presence/absence modelling has become an important tool in conservation biology. This study uses logistic regression to evaluate the independent effects of tropical forest cover and fragmentation on bird occurrence in eastern Guatemala. Logistic regression models were constructed for 10 species with varying response to habitat alteration. Predictive variables quantified forest cover, fragmentation and their interaction at three different radii (200, 500 and 1000 m scales) of 112 points where presence of target species was determined. Most species elicited a response to the 1000 m scale, which was greater than most species' reported territory size. Thus, their presence at the landscape scale is probably regulated by extra-territorial phenomena, such as dispersal. Although proportion of forest cover was the most important predictor of species' presence, there was strong evidence of area-independent and -dependent fragmentation effects on species presence, results that contrast with other studies from northernmost latitudes. Species' habitat breadth was positively correlated with AIC model values, indicating a better fit for species more restricted to tropical forest. Species with a narrower habitat breadth also elicited stronger negative responses to forest loss. Habitat breadth is thus a simple measure that can be directly related to species' vulnerability to landscape modification. Model predictive accuracy was acceptable for 4 of 10 species, which were in turn those with narrower habitat breadths.

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1. Introduction

Habitat destruction and fragmentation caused by wood extraction, forest plantations, crops and cattle ranching are the greatest threats to the maintenance of biological diversity in the Neotropics (Wilcove, 1985; Jullien and Thiollay, 1996; Turner, 1996), where the loss of forests is occurring at an accelerated rate (Bolin, 1977; Sader and Joyce, 1988; Kaimowitz, 1996; FAO, 2005). Habitat modification at the landscape scale mainly consists of two aspects: the loss of habitat *per se* and habitat fragmentation (Fahrig, 2003). The effects of habitat loss are obvious: when habitat is removed from the landscape, animals subsequently displaced can also be eliminated, producing a population decline (Bender et al., 1998). Fragmentation effects are less obvious, but could nonetheless be very important. Habitat fragmentation determines the subdivision and reduction in habitat area, a potential increase of edge effects and changes in the surrounding habitat matrix, effects by which landscape continuity can be reduced and thus threaten the survival of sensitive species (With, 1997).

At present, there is no general consensus concerning the relative importance of cover or configuration in determing species presence and survival, in particular regarding bird species persistence in modified landscapes (McGarigal and McComb, 1995; Villard et al., 1999; Fahrig, 2003; Westphal et al., 2003). It is important to distinguish between pure habitat loss and true fragmentation effects when assessing bird population responses, because resultant land management and conservation recommendations may differ (Schmiegelow and Mönkkönen, 2002).

Fragmentation effects on bird communities have been well documented in the boreal temperate zone (Robbins et al., 1989; Boulinier et al., 1998; Burke and Nol, 2000). For forest-interior species, fragmentation reduces their abundance and richness

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doi:10.1016/j.ecolmodel.2009.10.038

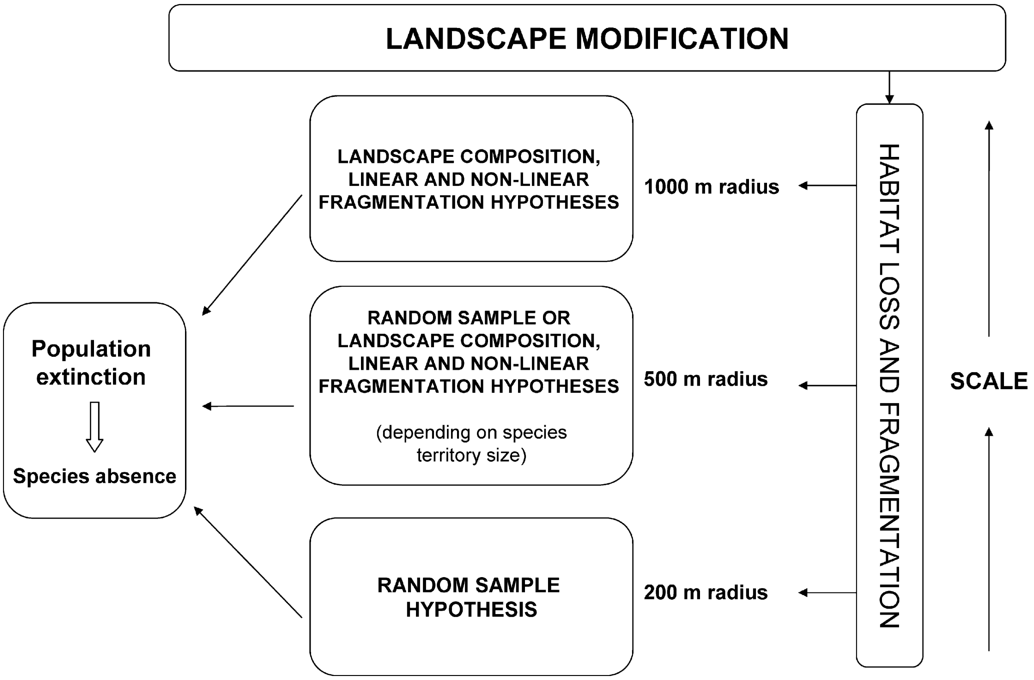

Fig. 1. Conceptual model of the effects of landscape modification on species presence in a particular site. See Section 1 for a description of the four hypotheses (random sample, landscape composition, and linear and non-linear landscape fragmentation hypotheses).

(Askins et al., 1990). In the Neotropics, studies of the effect of habitat fragmentation undertaken by the Biological Dynamics of Forest Fragments Project (BDFFP) have demonstrated that terrestrial insectivorous birds are particularly sensitive to disturbance, evidenced by the reduction in their abundance as patch size decreases and their local extinction in the smallest fragments (Stouffer and Bierregard, 1995; Gascon et al., 1999). Besides these few very important studies, other research on the effect of forest fragmentation on Neotropical birds, particularly at the landscape scale, is virtually non-existent, and the aforementioned studies are patch-oriented, as opposed to being landscape-oriented. More importantly, results from landscape-level effects of fragmentation demonstrated for temperate zone birds should not be extended directly to tropical birds, due to the fact that these possess different evolutionary and life histories, which make them vulnerable to a different suite of threats than those normally considered for birds from temperate regions (Stratford and Robinson, 2005). Species in temperate regions are under strong selection pressure from abiotic factors (e.g. climate) whereas in tropical regions biotic selection pressures are most important. Interactions with other species (plant and animal) have played a key role in shaping the behavioral adaptations of tropical birds (Stutchbury and Morton, 2001). Tropical birds have high nest predation, high adult survival and small clutch sizes (Skutch, 1954, 1960, 1969; Ricklefs, 1969; Stutchbury and Morton, 2001), as opposed to temperate birds. Food is abundant throughout the year in the tropics (Janzen, 1973, 1975), and this year-round availability means that most species are residents (non-migratory) and many that eat insects defend territories all year (Stutchbury and Morton, 2001). Also, unlike birds of temperate zones, tropical birds breed at all times of the year, breeding seasons are more protracted (Ricklefs, 1969), and are timed to coincide with fruit or insect abundance or reduced predation pressure, not climate *per se* (Stutchbury and Morton, 2001).

Typical tropical species also have a large number of complex and unique adaptations (Stutchbury and Morton, 2001). Many tropical birds tend to be sedentary or specialized in their habitat requirements, and such species are expected to have lower persistence in fragments, and are also the ones that are more extinction prone (Mac Nally et al., 2000; Sekercioglu, 2007; Sekercioglu and Sodhi, 2007). Area needs may be greater in the tropics, due to larger territory size (Terborgh et al., 1990; Robinson et al., 2000), and greater areas are often related to particular behavioral adaptations, like obligate army-ant following, and interspecific flocking (Terborgh et al., 1990). Species with these particular adaptations are often the first to disappear from fragments (Stouffer and Bierregard, 1995; Van Houtan et al., 2006; Ferraz et al., 2007). With respect to forest isolation through forest fragmentation, poor colonizers that rarely cross open areas, have relatively low patch occupancy in Amazonia, and thus are more vulnerable to fragmentation effects (Ferraz et al., 2007).

Given the complex nature of simultaneously evaluating the effects of landscape-level cover and configuration on population persistence, statistical presence/absence modelling (as a special case of generalized linear models, or GLM's) has become an important tool in conservation biology, improving the understanding of factors that determine the distribution of habitats, the species that occupy them and the human factors that lead to changes in the habitat (Guisan and Zimmermann, 2000; Guisan et al., 2002). Models represent ecological processes in simplified (Figs. 1 and 2), general ways that provide information on those factors responsible for the observed patterns (Johnson and Omland, 2004; Austin, 2007).

Habitat fragmentation indices are usually strongly correlated with habitat amount, thus making it difficult to evaluate area-independent fragmentation effects on species presence (Fahrig, 2003). This means that in real-world situations, habitat fragmentation usually increases with decreasing habitat cover (see Figure 2.5, page 19, in Lindenmayer and Fischer, 2006). Thus, most empirical studies have attempted to distinguish between these effects using statistical regression models (McGarigal and McComb, 1995; Trzcinski et al., 1999; Villard et al., 1999; Westphal et al., 2003). Our main objective was to evaluate the relative and independent contributions of landscape-scale cover and fragmentation of tropical forest in determining the presence of forest-dependent birds in the Caribbean region of Guatemala. To examine the potential relation between species' occurrence and landscape indices, we constructed occupancy-based habitat models using logistic regression, with for-

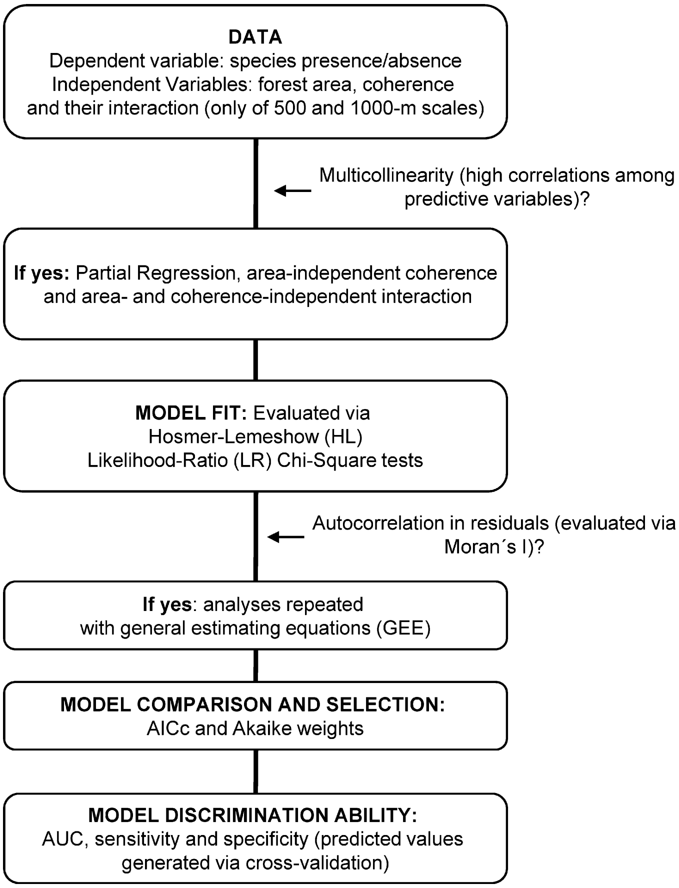

Fig. 2. Flow diagram of modelling procedure. See Section 2.4 for a detailed description of each procedure.

est area, fragmentation and their interaction as predictive variables. These relationships were examined at three different scales (200-, 500- and 1000-m scales).

Following Betts et al. (2006b), models with area and fragmentation variables at different scales were related to a series of hypotheses concerning population responses to landscape modification. At the smallest scale, we sought a response related to the “random sample hypothesis” (Haila, 1983), which states that only factors (specifically the amount of suitable habitat) at the scale of an individual territory are important in determining habitat quality. This hypothesis also implies that species have high dispersal capabilities, and are able to find patches with a size that corresponds to their territory size. Alternatively, a response related to scales greater than territory size would correspond to the so-called “landscape composition hypothesis”, which states that species respond to the amount of suitable habitat, but at larger spatial scales than the individual territory (Fahrig, 2003; Betts et al., 2006b). We also sought evidence for the “landscape fragmentation hypothesis”, which expects populations to decline with increasing fragmentation, independent of the effects of habitat loss (Villard et al., 1999; Betts et al., 2006b). Finally, an area-dependent effect of fragmentation is described by the “non-linear landscape fragmentation hypothesis”, which states that landscape fragmentation is important only below some critical amount of habitat (Andrén, 1994b; Fahrig, 1998; Betts et al., 2006b). This would result in multiplicative (non-linear) effects of fragmentation on habitat loss, i.e., a statistical interaction between landscape configuration and composition (Trzcinski et al., 1999; Betts et al., 2006b).

In theoretical studies, the relative importance of fragmentation appears to depend on the life-history traits of hypothetical species (Fahrig, 1998; With and King, 1999). Mixed results of fragmentation studies have been attributed to differences in such traits (Ewers and Didham, 2005). We investigated the relationship of species responses to fragmentation and one particular life-history trait, habitat breadth, because of its fundamental association to species' dispersal ability. Assuming that dispersal is a key aspect of species' persistence in fragmented landscapes, the important question is whether a species is able to disperse through (and survive in) the landscape matrix (Opdam, 1991; Fahrig, 2001; Ricketts, 2001). Terrestrial habitats are often surrounded by a complex mosaic of other cover types, which may differ in their resistance to the movement of individuals among habitat patches (Gustafson and Gardner, 1996; Ricketts, 2001; Laurance et al., 2002). A species' ability to use matrix habitats may affect their vulnerability in fragmented landscapes (Gascon et al., 1999). A direct prediction of this hypothesis is that a species with a wider habitat breadth will find less resistance to move through the matrix and therefore will be less susceptible to fragmentation effects. In terms of resources, species that are able to exploit secondary habitats might have higher survival probability (at the individual and population level), supplementing their resource intake by using a substitutable resource in nearby patches of secondary habitats (landscape supplementation, Dunning et al., 1992).

In our modelling approach, we used a combination of traditional null hypothesis tests (NHT) and information-theoretic model-selection approaches, specifically the Akaike Information Criterion (AIC), for model-selection (Luckacs et al., 2007; Stephens et al., 2005). The Kullback–Leibler information-theoretic (KLIT) framework cannot assess model goodness-of-fit, which in contrast is provided for by the NHT framework. Alternatively, KLIT methods allowed us to compare models of different scales, comparisons not possible with inferential approaches: with NHT, only comparisons of reduced models which are nested within full models are possible (Agresti, 1996). From a practical conservation perspective, we evaluated the model's ability in predicting species presence and absence, and discuss their applicability to the study region.

2. Methods

2.1. Study area

The study was conducted in Cerro San Gil Watershed Protection Reserve (hereafter CSGWPR), in the Caribbean region of Guatemala. The predominant natural vegetation is very humid tropical and subtropical forest (Holdridge, 1967), with an average annual rainfall of 3010 mm and a mean annual temperature of 26.7 °C (INSIVUMEH, 2005). Originally, the study area was completely covered by mature tropical forest, and since the late 1970s, 65% of it has been converted to cattle pasture or cropland (dominated by corn) and more recently to forest plantations. Forest structure consisted of two well-defined canopies and an understory vegetation layer ($n = 95$ measured forest patches). The average height of the three tallest trees (±S.D.) was 16.5 ± 4.2 m. Average cover and density values for the primary canopy were 13.9 ± 14% and 11.9 ± 12.2%, respectively, and for the secondary canopy, 40.6 ± 23.2% and 36.6 ± 20.5%, respectively. The three vegetation layers were dominated by evergreen trees (67.0 ± 45.3%, 71.5 ± 35% and 66.3 ± 32.4% dominance in primary and secondary canopy and understory, respectively), but palm tree dominance increased gradually from the top to bottom layer, from 4.0 ± 15.7% in the primary canopy to 13.2 ± 14.8% in the understory. Ground cover was dominated by saplings (36.3 ± 19.1% cover) and dead vegetation (38.8 ± 20.5%).

In 1996, 112 point count locations separated by 800 m from each other were established on secondary roads, within and in immediate vicinity of CSGWPR. All points are sampled once a year as

Table 1
Life-history description of bird species.

Species name	Feeding stratus[a]	Foraging guild[a]	Body mass[a] (g)	Territory radius (m)[b]	Habitats[c]					
					TEF	SF	WAH	ESG	OAH	Habitat breadth[e]
Patagioenias nigrirostris Short-billed Pigeon	C	F	150.0	203.7	X	X	X			390
Trogon melanocephalus Black-headed Trogon	M/C	O	90.0	209.9	X	X	X	X	X	212
Momotus momota Blue-crowned Motmot	U/M	O	120.0	212.1	X	X	X			367
Ramphastos sulfuratus Keel-billed Toucan	C	O	500.0	299.1	X	X	X	X		282
Xiphorhynchus flavigaster Ivory-billed Woodcreeper	U/M	I	60.0	203.1	X	X	X	X		335
Hylophilus decurtatus Lesser Greenlet	M/C	I	9.0	228.2	X	X	X			351
Thryothorus maculipectus Spotted-breasted Wren	U/M	I	17.0	429.9	X	X	X	X		314
Dendroica magnolia Magnolia Warbler	M/C	I	8.5	N/A[d]	X	X	X	X	X	247
Saltator atriceps Black-headed Saltator	U/C	G	85.0	460.8	X	X	X	X		243
Psarocolius montezuma Montezuma Oropendola	C	F	520.0	198.4	X	X	X			270

Stratus: C, canopy; M/C, mid/canopy; U/M, understory/mid; U/C, understory/canopy. Foraging guild: F, frugivore; G, granivore; I, insectivore; O, omnivore. Habitats: TEF, tropical evergreen forest; SF, secondary forest; WAH, wooded agricultural habitats; ESG, early second growth; OAH, open agricultural habitats.

[a] Information on foraging stratus; feeding guild and body mass from Stotz et al. (1996) and Stiles and Skutch (1989).

[b] Territory radius calculated from density estimates taken from Robinson et al. (2000), Robinson and Terborgh (1997), Thiollay (1994), and Terborgh et al. (1990). When territory size estimates for a species was not available, calculations from species belonging to the same genus were used.

[c] Habitat use information from Cerezo et al. (2009), Smith et al. (2001), Estrada et al. (1997), Stotz et al. (1996), and Stiles and Skutch (1989). *T. maculipectus* and *S. atriceps* are reported as edge specialists in Stotz et al. (1996) and Rotenberg (2007).

[d] Territory size information for *D. magnolia* on wintering grounds not available.

[e] Habitat breadth is quantified using species' positions (i.e., scores) on axis 1 of a detrended correspondence analysis, which represented a primary forest–secondary riparian forest–hedgerow–pasture gradient, data from Cerezo et al. (2009).

part of a bird monitoring effort, during a 2-week period that took place during the last week of April and the first week of May. For this study, data from 1998 to 2001 was used. Unlimited-radius, 5-min point counts were conducted at each point and the presence of all birds detected (visually and/or aurally) was noted. Counts were conducted by six field biologists and technicians, four of whom had been trained by the two most experienced observers during the two previous years of surveys. Secondary roads cross landscapes with varying degrees of tropical forest cover (varying from 70% to 5%) and fragmentation. As opposed to rural roads in more developed countries (Keller and Scallan, 1999; Bart et al., 1995), these are not dominated by particular roadside habitats, but are in close contact with remaining forest habitat (in many cases within forest patches, or within a 50–100-m radius of patch edges) are relatively narrow (3–6 m) and have very low human population density and transit. Thus, although roadside perturbations biased our sample to some degree, the level of bias was most likely small and consistent across sites.

2.2. Evaluation of forest cover and configuration at the landscape scale

A Geographic Information System (G.I.S.) was used to produce a non-supervised land use/land cover classification, using a Landsat 5 TM image from the year 2001. For the natural forest class, landscape accuracy was 89%, evaluated via comparison of visual estimations of forest cover in a 200-m radius of sample points and forest cover in this radius from the satellite image classification. Around each of the 112 sample points, concentric 200-, 500- and 1000-m buffers were created (distances are radii). Within each "mini-landscape", we calculated the proportion of forest cover in hectares. Proportional forest cover values for the 200-, 500- and 1000-m scales were 0.22 ± 0.20, 0.25 ± 0.18, and 0.48 ± 0.28, respectively.

To measure forest fragmentation, we used the coherence index (Jaeger, 2000). The degree of coherence is defined as the probability that two animals placed in different areas somewhere in the region of investigation might find each other, and is calculated as:

$$C = \sum_{i=1}^{n} \left(\frac{A_i}{A_t}\right)^2,$$

with n is the number of patches; A_i is the sizes of the n patches ($i = 1, \ldots, n$); A_t is the total area of the region (Jaeger, 2000). The index increases as landscape fragmentation decreases, and in comparison to other fragmentation measures, has the following desirable properties: (1) low sensitivity to very small patches, as opposed to the mean patch size; (2) monotony of its reaction to different fragmentation phases (perforation, incision, dissection, dissipation, shrinkage and attrition, *sensu* Forman, 1995; Jaeger, 2000), as opposed to the number of patches, which has a non-linear response to fragmentation (Gustafson and Parker, 1992; Saura and Martínez-Millán, 2000; Fahrig, 2003); (3) ability to distinguish spatial patterns; (4) mathematical simplicity (Jaeger, 2000). Furthermore, we did not use any of the traditional fragmentation indices because these were highly correlated to forest area (correlations with forest area and: (1) mean patch size, Spearman's $\rho = 0.92$–0.96, depending on the scale; (2) total edge, $\rho = 0.82$–0.89; (3) mean patch edge, $\rho = 0.88$–0.90). Coherence values for the 200-, 500- and 1000-m scales were 0.87 ± 0.20, 0.62 ± 0.27, and 0.48 ± 0.28, respectively.

2.3. Description of bird species

Our study species are described in Table 1. The criteria for chosing these species were the following: (1) they are common or relatively common species in the study region and tropical

Table 2
Absolute and relative (in parentheses) yearly and total detection frequencies for study species.

Species name	1998	1999	2000	2001	Total
P. nigrirostris	5 (0.04)	4 (0.03)	5 (0.04)	9 (0.08)	18 (0.16)
T. melanocephalus	22 (0.19	21 (0.18)	24 (0.21)	23 (0.20)	68 (0.60)
M. momota	6 (0.05)	5 (0.04)	7 (0.06)	4 (0.03)	31 (0.27)
R. sulphuratus	10 (0.08)	5 (0.04)	7 (0.06)	0 (0.00)	29 (0.25)
X. flavigaster	5 (0.04)	2 (0.01)	3 (0.02)	3 (0.02)	30 (0.26)
H. decurtatus	5 (0.04)	8 (0.07)	9 (0.08)	9 (0.08)	19 (0.16)
T. maculipectus	12 (0.10)	9 (0.08)	17 (0.15)	8 (0.07)	44 (0.39)
D. magnolia	10 (0.08)	15 (0.13)	8 (0.07)	13 (0.11)	41 (0.36)
S. atriceps	14 (0.12)	12 (0.10)	19 (0.16)	17 (0.15)	52 (0.46)
P. montezuma	21 (0.18)	27 (0.24)	24 (0.21)	22 (0.19)	60 (0.53)

Total detections equal the number of points ($n = 112$) in which the species was detected in at least 1 year.

evergreen forest is their main habitat type (Cerezo et al., 2009; Stotz et al., 1996); (2) they are reported as relatively tolerant of edges and secondary forest habitats (Stotz et al., 1996; Stiles and Skutch, 1989), adaptations which could aid their persistence in deforested landscapes (Harris and Pimm, 2004); (3) their songs and calls are well known by observers, and are detectable at large distances; (4) they represent the local bird community in terms of ecological and taxonomic diversity; (5) they have a relatively well known life history, including records of territory size and density (Terborgh et al., 1990; Robinson and Terborgh, 1997; Robinson et al., 2000). Species' tolerance to secondary habitats varied (Table 1). We quantified habitat breadth using data from Cerezo et al. (2009): species' positions (i.e., scores) on the principal axis of a detrended correspondence analysis (DCA), which represented a pasture–hedgerow–secondary riparian forest–primary forest gradient. The detrended correspondence analysis was generated from a sites by species matrix, which contained relative abundance values for species detected in the study in 17 sites (5 primary forest and riparian, 3 hedgerow and 4 pastures sites). Species with higher principal axis values were more restricted to primary forest.

All except one (Magnolia Warbler, *Dendroica magnolia*) are year-round residents. We included the Magnolia Warbler because it is a very common winter resident, we had an adequate sample size for it, and represented neotropical migrants, which are a significant and very important proportion of the local avifauna (Cerezo et al., 2009).

2.4. Statistical analysis

To construct occupancy-based habitat models, we used logistic regression, which evaluates the functional relationship between a binomial dependent variable and one or multiple independent variables, which may be discrete or continuous (Trexler and Travis, 1993; Hosmer and Lemeshow, 1989). Logistic regression results also indicate the predictive power of the independent variables for the dependent variable. The response variable was species presence/absence, and candidate predictive variables were the proportion of forest cover, fragmentation (measured via the coherence index) and their interaction at 200-, 500-, and 1000-m radii from each sample point. An area with a 200-m radius corresponded approximately to species' territory sizes in most cases (Table 1). From a practical perspective, spatially explicit models can increase predictive ability conferred by using appropriate scales of habitat characterization at the landscape level (Dunning et al., 1995; Orrock et al., 2000). The two largest extents have been found to adequately predict forest bird presence and abundance in North America (Betts et al., 2006a; Drapeau et al., 2000).

We assumed that a particular focal species was present in any given point if it was detected in at least 1 year during the study period (1998–2001). Thus, we did not consider inter-annual effects on occupancy, since our interest was whether the particular landscape type represented by the point was usable or not by the species in any moment in time, and not to evaluate temporal dynamics in occupancy. More importantly, analyses of data relying on point count surveys have been strongly criticized because they are conducted without attempting to estimate or adjust for detection probability (Barker and Sauer, 1995; Farnsworth et al., 2002). Gu and Swihart (2004) determined that bias in parameter estimation of logistic regression models occurred in both analytic and simulation studies, but do not recommend any (analytical) way of correcting this bias in such models. What they do recommend is incorporating multiple sampling occasions into presence-absence sampling protocols, as MacKenzie et al. (2002) have recommended. We acknowledge that our sampling methodology does not permit direct estimation of detection probability, but we believe that considering as a presence the detection of the species in at least 1 of the 4 years reduced the effects of falsely recorded absences by at least a factor of three on model parameter estimation (Table 2). Gu and Swihart (2004) also note that the lower the species detection probability, the greater the bias parameter estimates. Based on our experience, we believe that detection probability is relatively high for our study species, and thus the aforementioned biases are expected to be low. Lastly, we believe that our models are conservative, in the sense that for species with lowest detection probabilities, they may overestimate the effects of forest loss and fragmentation on species presence, i.e., that species appear to be more vulnerable to these effects than they truly are. From a conservationist perspective, this is far better than saying that species are less vulnerable to landscape modification effects than what they truly are.

For each scale, we constructed one model with both cover and coherence variables as predictive variables (henceforth, "area-fragmentation model"), two simple models with either area (henceforth, area model) or coherence (henceforth, "fragmentation" model) as a single independent variable, and one model with both effects and an interaction term (henceforth, "interaction model"). We did not construct models with an interaction term for the 200-m scale since it was highly correlated with the coherence index (Spearman's $\rho = 0.98$, see below for our treatment of multicollinearity). Thus, for each species, we constructed 11 models, 3 for the 200-m scale, and 4 for each one of the larger scales.

The second-order Akaike Information Criterion ($\mathrm{AIC_c}$, advocated when $n/K < 40$, where n is the sample size and K is the number of estimated parameters) and Akaike weights (w_i) were then used to choose the best-fitting models from the set of candidate models (Anderson et al., 2000; Burnham and Anderson, 1998, 2001). The AIC belongs to a family of model-selection criteria that consider the fit as well as the complexity of the model, and allows comparison of several models simultaneously (Johnson and Omland, 2004). AIC values reflect the amount of "information" lost when a model is used to approximate conceptual reality; thus, the model with the lowest AIC value is selected as the best model (Burnham and

Anderson, 1998). When differences between AIC values are small (less than 2 AIC units), Akaike weights (termed w_i) can be used as indicators of the strength of evidence for each model. The w_i is interpreted as the approximate probability that model i is the best model in the set of models being considered (Anderson et al., 2000). We show results for the three models with greatest support. These models usually accounted for more than 70% of support of the 11 models constructed for each species (sum of Akaike weights for the three models). Models did not exhibit overdispersion, according to the highest estimated single variance inflation factor ($\hat{c}$) of the most parameterized models (models for the 500- and 1000-m scales with an interaction term), estimated as the ratio of the deviance statistic and its degrees of freedom ($\hat{c}$ = deviance/d.f., maximum value of 1.42 for the interaction model, 500-m scale, for *Saltator atriceps*).

Logistic regression is free of several assumptions related to ordinary least-squares regression (Agresti, 1996; Allison, 1999), but has alternative assumptions which must be met: the model must be correctly specified (the logit must be linearly dependent of the predictive variables), multicollinearity must be avoided, and observations must be independent. To evaluate correct model specification, we used the Hosmer and Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 1989). Non-significant results of this test indicate a correct model specification (Allison, 1999). We used the likelihood-ratio chi-square statistic to test the null global hypothesis that all explanatory variables have coefficients equal to zero (Allison, 1999; Agresti, 1996). We also used Wald chi-square statistics to test the significance of individual model coefficients ($\alpha = 0.1$) (Agresti, 1996).

In order to detect and minimize problems associated with multicollinearity, correlations between proportion of forest area, coherence, and their interaction were evaluated via the Spearman correlation coefficient. When correlations were ≥ 0.6, as was the case for the 500- and 1000-m scales, we performed partial linear regression analysis (Legendre and Legendre, 1998). When coherence was highly correlated with forest area, area was used as the predictive variable and forest coherence as the response variable, and when the interaction was highly correlated with coherence, coherence was used as the independent variable and the interaction as the dependent variable. We then used the residuals of these partial regressions as independent indexes of landscape coherence and/or the interaction term.

Given the nature of our sampling scheme, we considered that our observations lacked spatial dependency, especially at small distances among points. The presence of spatial autocorrelation in a dataset can have serious negative consequences on hypothesis testing and prediction because it violates the assumption of independently and identically distributed errors and hence inflates type I errors (Lichstein et al., 2002; Dormann et al., 2007), causing a form of pseudoreplication by overestimating effective degrees of freedom (Dutilleul et al., 1993; Carl and Kühn, 2007). Spatial autocorrelation in residual variance, i.e. variance not explained by the predictor variables, is problematic, particularly in hypothesis testing, since estimated error or variance terms are used in calculating test statistics. Thus, it is important to determine if spatial autocorrelation exists in the residuals, not in the raw dependent variable (Betts et al., 2006a). We used correlograms of Moran's I (Fortin and Dale, 2005) to test for autocorrelation in deviance residuals of the 3, best-fitting models for each species, at 500-m lag distances, using program PASSAGE version 1.0 (Rosenberg, 2001). If autocorrelation in model residuals was detected at any of the lag distances, we used general estimating equations (GEE) to account for spatial autocorrelation in data analyses (Carl and Kühn, 2007; Dormann et al., 2007). When responses are measured repeatedly through time or space, the GEE method takes correlations within "clusters" of sampling units into account by means of a parameterized correlation matrix, while correlations between clusters are assumed to be zero (Dormann et al., 2007). In our study, clusters were groups of sample points, and the minimum distance between clusters was 2000 m, the lag distance at which spatial autocorrelation was less than 0.1 or −0.1. Most models assuming spatial independence elicited spatial autocorrelation in residuals ($0.1 < r < 0.2$, Fig. 3). Consequently, all model coefficients were estimated using the GEE estimation method. All GEE analyses were carried out using the GENMOD procedure in SAS statistical package (SAS Institute, 1999).

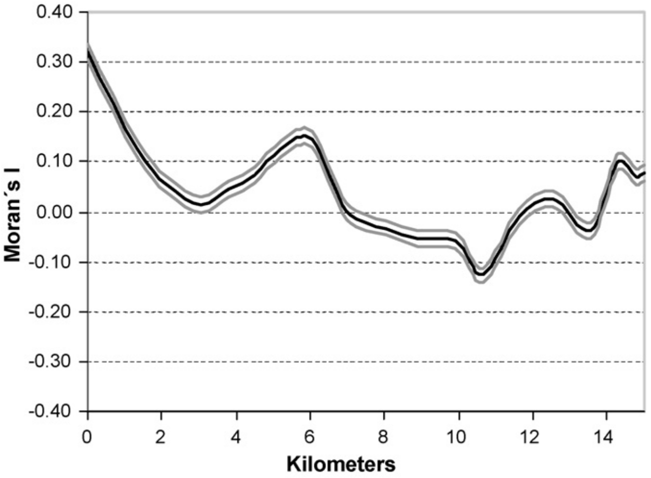

Fig. 3. Example of autocorrelation in model residuals, using Moran's I (with 95% confidence interval). The graph corresponds to the interaction model at the 1000 m scale for *X. flavigaster*. The largest autocorrelation is at scales smaller than approximately 2 km.

We validated models using a cross-validation method (Pearce and Ferrier, 2000; Bonn and Schröder, 2001; Betts et al., 2006a). Data points were randomly divided into 10 equal groups, models were fitted using 90% of the data and predictions were generated for the remaining 10%. Thus, predicted values, the probability of presence, were generated for all points independently of training data. The discrimination performance of logistic regression models is often assessed by examining the agreement between predictions and actual observations (Pearce and Ferrier, 2000). To determine model prediction accuracy, we evaluated models in terms of their sensitivity, the proportion of correctly classified presences, and specificity, the proportion of correctly classified absences (Fielding and Bell, 1997; Pearce and Ferrier, 2000). In wildlife habitat models, a species is predicted to be present or absent at a site based on whether the predicted probability for the site is higher or lower than a specified threshold probability value, which in turn depends on the presence/absence ratio, or species rarity in the sample (Pearce and Ferrier, 2000). We used a critical threshold or cutoff value where sensitivity and specificity were approximately the same (P_{fair}, Schröder. and Richter, 1999, Fig. 4).

We also used the receiver-operating characteristic (ROC) curve as an independent measure of model accuracy, or discrimination ability (Guisan and Zimmermann, 2000; Pearce and Ferrier, 2000). A ROC curve was obtained by plotting the true positive proportion of correctly predicted occurrences on the y-axis against the false positive proportion of correctly predicted absences on the x-axis (Hanley and McNeil, 1982). The area under the ROC curve (AUC) was used to test a greater significance than the area under a random model, with $\text{AUC}_{\text{crit}} = 0.5$, i.e., the chance performance of a model lies on the positive diagonal in the ROC graph (Schadt et al., 2002). The AUC can be interpreted as the probability that a model will correctly distinguish between two observations, one positive (in our case, species presence) and the other negative (absence) (Hanley and McNeil, 1982; Pearce and Ferrier, 2000). An AUC value between 0.7 and 0.9 indicates that a model has reasonable discriminatory ability (Pearce and Ferrier, 2000).

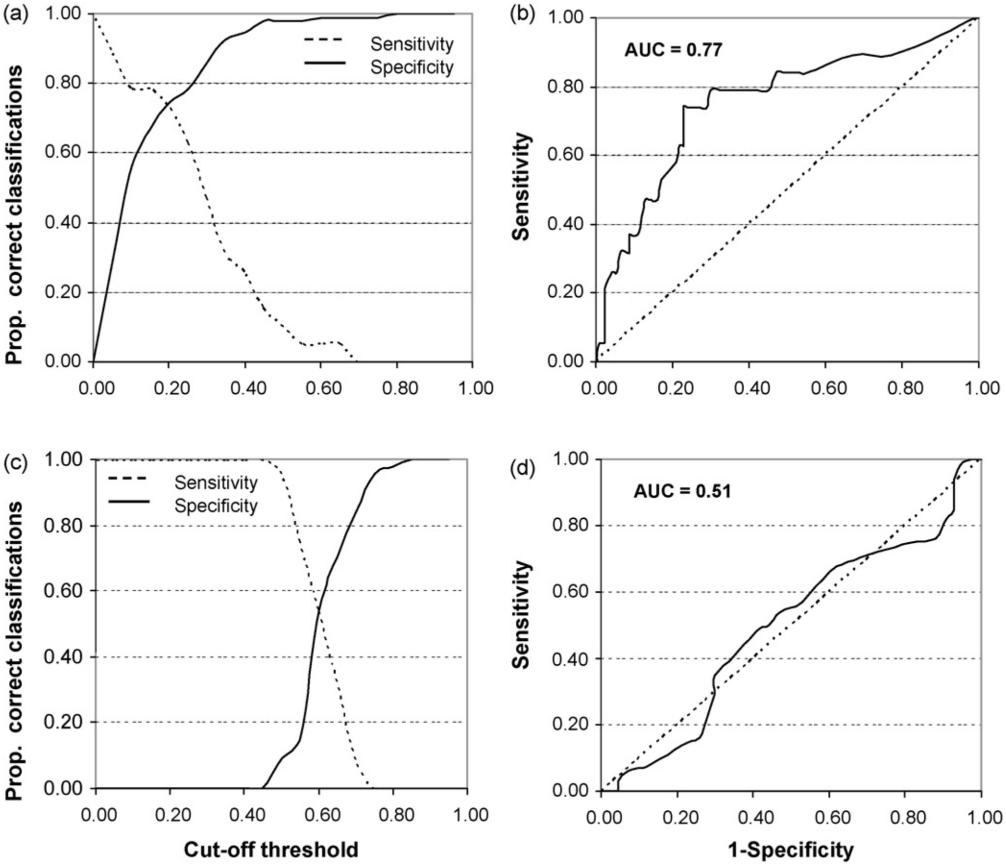

Fig. 4. Plots of the proportion of correctly predicted presences (sensitivity) and absences (specificity) (a and c) and ROC curve (b and d) for *H. decurtatus* (a and b) and *T. melanocephalus* (c and d). The critical threshold or cut-off value used is where sensitivity and specificity were approximately the same (see Section 2.4 for details).

We investigated correlations between species' habitat breadth (i.e., number of secondary habitats, all habitats except tropical evergreen forest, see Table 1) and model fit (mean AIC of three models), prediction accuracy (mean AUC of three models), and model coefficients, using Pearson's correlation coefficient (relationships appeared linear in graphs). For each species, we calculated a weighted average of model coefficients for the three models (weighted by w_i).

3. Results

All models except the area model for *Ramphastos sulphuratus* had non-significant results in the Hosmer–Lemeshow (HL) GOF statistic, indicating adequate model specification. The likelihood-ratio (LR) statistic was significant ($\alpha = 0.05$) or marginally significant ($\alpha = 0.10$) for all models except for *Trogon melanocephalus* and *D. magnolia*. Table 3 shows results for the three models with strongest support, based on Akaike weights, for each study species.

All species except *T. melanocephalus* and *D. magnolia* responded mainly to the 1000 m scale: mean Akaike weights (for models in Table 3) for this scale varied between 0.19 and 0.25, while mean Akaike weights for models for the 200 and 500 m scales varied between 0.00 and 0.03, and 0.00 and 0.07, respectively (Fig. 5). Except for these two species, support (sum of Akaike weights) for 1000 m scale models ranged between 0.66 for *S. atriceps* and 0.98 for *M. momota*. In many cases, the likelihood-ratio test, as a test of general model fit, was not significant for most species at the 200 and 500 m scales (Appendix 2).

Most species consistently responded positively to the proportion of forest area, but responses to landscape fragmentation varied. When the coherence coefficient was significant (Table 3), most species responded negatively to landscape fragmentation (i.e., positively to landscape coherence). In most models that included the interaction term, the coherence coefficient was non-significant.

When considering the model with the highest Akaike weight, area models had strongest support for five species. The interaction model had the highest weight for two species, the area-fragmentation model for two species, and the fragmentation model for one species. Nevertheless, none of the models with highest Akaike weights had much stronger support than the second and third best-supported models. Only for *R. sulphuratus* was the difference in AIC between the best-supported model and the third model greater than 2, indicating that, for the other species, models 2 and 3 had substantial support (according to criteria described in Anderson et al., 2001). On average, the area-coherence model had approximately the same support as area-only models (area-coherence model mean $w_i = 0.27 \pm 0.15$ S.D. vs. area model mean $w_i = 0.28 \pm 0.19$; interaction model mean $w_i = 0.22 \pm 0.14$). On average, the best-supported model had 3.7 times more support than the least-supported of the three models (evidence ratio, calculated as w_1/w_3, Luckacs et al., 2007; Anderson et al., 2001).

With respect to the effect size of different predictive variables, area and fragmentation effects were on average larger at the 1000 m scale than the other two scales, and interaction effects were much larger at this scale than at the 500 m scale (Fig. 6).

Relative model fit was generally much worse for species with greater habitat breadth, evidenced by a significant positive correlation between AIC_c and habitat breadth (Table 4). This is clearly demonstrated by *T. melanocephalus* and *D. magnolia*, both of which according to the literature make ample use of secondary habitats

Table 3
Model results for three models with highest Akaike weights (greatest support); Model indicates the parameters in models (COHR, coherence; INT, interaction); AIC values, Akaike weights, significance of lilkelihood-ratio (LR) and Hosmer–Lemeshow (HL), area under the receiver-operating curve (AUC), sensitivity, and specificity values are shown.

Species	Model	Scale	LR *p*-value	HL *p*-value	AIC$_c$	w_i	AUC	Sens.	Spec.
P. nigrirostris	Area* + COHR* + INT^{NS}	1000	<0.01	0.74	95.24	0.43	0.62	0.61	0.57
	Area** + COHR**	1000	<0.05	0.75	96.94	0.19	0.63	0.61	0.60
	Area***	1000	0.08	0.05	97.74	0.12	0.59	0.61	0.61
T. melanocephalus	COHR***	500	0.19	0.36	151.50	0.25	0.47	0.46	0.49
	Area*	1000	0.14	0.13	152.04	0.19	0.50	0.54	0.53
	Area^{NS} + COHR***	500	0.33	0.96	153.33	0.10	0.47	0.49	0.49
M. momota	Area***	1000	<0.0001	0.63	112.34	0.63	0.77	0.68	0.69
	Area*** + COHR^{NS}	1000	<0.0001	0.96	114.19	0.25	0.76	0.71	0.70
	Area*** + COHR^{NS} + INT^{NS}	1000	<0.0001	0.48	115.94	0.10	0.76	0.68	0.68
R. sulphuratus	Area*** − COHR***	1000	<0.0001	0.17	108.40	0.61	0.75	0.72	0.73
	Area*** − COHR** − INT^{NS}	1000	<0.0001	0.14	110.44	0.22	0.73	0.72	0.73
	Area***	1000	<0.0001	0.02	111.35	0.14	0.76	0.73	0.73
X. flavigaster	Area** + COHR*	1000	<0.01	0.10	126.70	0.34	0.66	0.67	0.65
	Area***	1000	<0.01	0.36	126.77	0.32	0.63	0.63	0.65
	Area** + COHR^{NS} + INT^{NS}	1000	<0.05	0.46	128.81	0.12	0.64	0.63	0.65
H. decurtatus	Area**	1000	<0.0001	0.72	87.87	0.57	0.76	0.74	0.74
	Area** + COHR^{NS}	1000	<0.0001	0.65	89.54	0.25	0.75	0.74	0.73
	Area** − COHR^{NS} + INT**	1000	<0.0005	0.87	90.67	0.14	0.73	0.72	0.71
T. maculipectus	Area***	1000	<0.0005	0.23	139.94	0.43	0.70	0.66	0.66
	Area*** − COHR^{NS}	1000	<0.001	0.56	141.18	0.23	0.69	0.66	0.66
	Area*** − COHR^{NS} + INT^{NS}	1000	<0.001	0.64	142.00	0.15	0.69	0.63	0.66
D. magnolia	Area^{NS}	200	0.12	0.56	148.76	0.28	0.50	0.56	0.54
	Area^{NS}	500	0.46	0.70	150.43	0.12	0.42	0.46	0.47
	COHR^{NS}	1000	0.45	0.85	150.67	0.11	0.33	0.37	0.36
S. atriceps	Area** + COHR^{NS} + INT***	1000	<0.05	0.70	152.28	0.45	0.60	0.56	0.56
	Area***	1000	<0.05	0.33	154.14	0.18	0.57	0.56	0.56
	Area**	500	0.20	0.38	155.34	0.10	0.53	0.52	0.52
P. montezuma	Area*	1000	<0.01	0.34	148.40	0.48	0.64	0.62	0.61
	Area* − COHR^{NS}	1000	<0.01	0.32	149.95	0.22	0.62	0.62	0.61
	Area* − COHR^{NS} − INT^{NS}	1000	<0.01	0.58	150.73	0.15	0.63	0.61	0.61

NS, not significant.

* Significance levels: $0.05 < p < 0.1$.

** Significance levels: $0.01 < p < 0.05$.

*** Significance levels: $p < 0.01$.

(Table 1). All models for these two species were not significant according to the likelihood-ratio chi-square statistic test (Table 3).

Significant correlations ($p \leq 0.1$) were found between habitat breadth, and the intercept and area model coefficients. There was no significant relationship between the coherence and interaction coefficients and habitat breadth (Table 4).

Best-supported models for 4 of 10 species had an acceptable predictive accuracy (AUC ≥ 0.7; *M. momota*, *R. sulphuratus*, *H. decurtatus* and *T. maculipectus*). For theses species, the proportion of correctly predicted presences varied between 0.63 and 0.74, and the proportion of predicted absences, between 0.66 and 0.74 (Table 3). The AUC was also significantly and negatively correlated with species' habitat breadth (Table 4): models for species that were more restricted to tropical forest were more accurate in predicting species presence/absence.

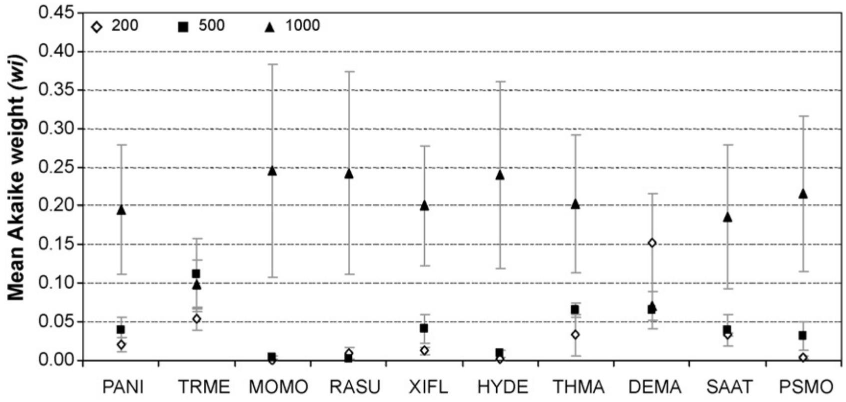

Fig. 5. Mean Akaike weights by scale. Values were calculated averaging Akaike weights for all models for each scale, for each species. Abbreviations for species are the first two letters of the genus and specific name.

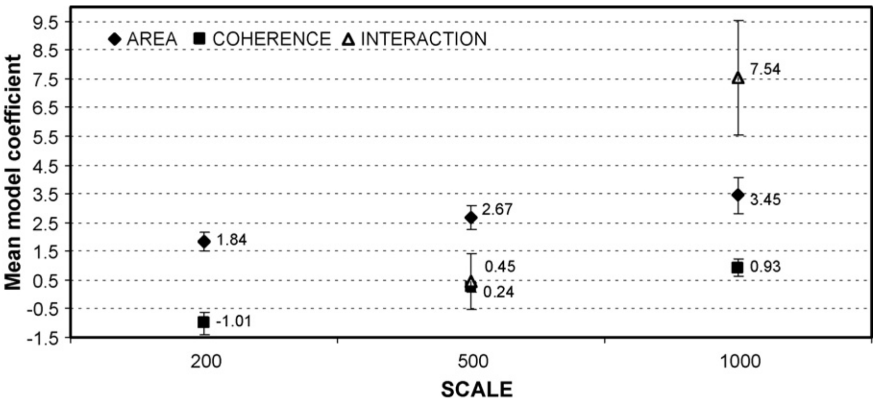

Fig. 6. Mean model coefficients for area, fragmentation and interaction effects. An interaction term was only included in models for 500 and 1000 m scales. Values shown were calculated by first averaging model coefficients for the top three models for each species, weighted by corresponding Akaike weights. These values were then averaged by scale over all species.

4. Discussion

Our adoption of the concept of multiple working hypotheses (Chamberlin, 1965; Anderson et al., 2001; Burnham and Anderson, 2001; Betts et al., 2006b), and the KLIT framework allowed us to simultaneously contrast the random sample, landscape composition and linear and non-linear landscape fragmentation hypotheses, *sensu* Betts et al. (2006b). This framework allowed us to contrast models with variables corresponding to different scales. Our results indicate that bird response to landscape forest loss and fragmentation at the 1000-m scale was much stronger than at the two smaller scales. Consequently, most of the evidence from this study does not support the random sample hypothesis. The random sample hypothesis predicts, for statistical reasons, that common species are the only species to be found on small islands, whereas rare species will mainly occur on large islands (Andrén, 1994a). It follows that if there is no effect of habitat modification at scales larger than the territory size, then all species which have a territory size corresponding to the patch size should be present in the patch, irrespective of the amount or degree of fragmentation at larger scales. In this sense, we believe that having found an almost general species' response to a scale which, for most species, is approximately 20 times greater than the average territory size (12.6 ha is the area corresponding to the 200 m radius and 314 ha to the 1000-m radius), is evidence of a habitat modification effect at scales greater than the territory size. An exception is the third most-supported model for *S. atriceps*, the area model at the 500 m scale, which corresponded approximately to its territory radius, Table 1; nonetheless, this species responded more to the 1000 m scale (Table 1). More importantly, this finding may imply that for a particular site to be occupied, species need a larger amount of forest at scales greater than territory size to reach and occupy the site, i.e., they may need forest to disperse to the site. This finding thus has important conservation implications: the persistence of these species in modified landscapes is probably mediated by extra-territorial movements, such as dispersal (Rolstadt, 1991; Wiens et al., 1993; Sutherland et al., 2000; Norris and Stutchbury, 2001; D'Eon et al., 2002; Bowman, 2003). Other studies have found bird responses to habitat modification at scales larger than territory size in North America (Drapeau et al., 2000; Lichstein et al., 2002; Betts et al., 2006a) and in Australia (Westphal et al., 2003). These results also agree with metapopulation (Hanski, 1998) and source-sink (Pulliam, 1988) theoretical studies: metapopulation persistence or population persistence in sink habitats is directly dependent on extra-territorial movements, and specifically on species' dispersal ability (Opdam, 1991).

Table 4
Pearson correlations between model statistics and species' habitat breadth.

	Habitat breadth	*p*-Value
AIC	−0.87	0.01
AUC	0.71	0.03
Intercept	−0.79	0.02
Area	0.55	0.10
Coherence	0.15	0.65
Interaction	0.46	0.17

Coefficients for each species were calculated as averages weighted by Akaike weights (w_i) from the three best-fitting models.

Our results also show that the proportion of forest area is generally more important than landscape fragmentation in explaining bird species occurrence, a result that agrees with previous studies (McGarigal and McComb, 1995; Westphal et al., 2003; Fahrig, 2003). Nonetheless, there is also strong evidence of species responses to fragmentation. Area-independent landscape fragmentation was a significant predictor in models with highest Akaike weights for three species, and in *T. melanocephalus*, landscape coherence was the only predictor in the most-supported model. We also found evidence for the non-linear fragmentation hypothesis: species are affected by forest fragmentation, but effects are stronger at lower levels of forest cover. This conclusion has strong support in 2 of 10 study species, *P. nigrirostris* and *S. atriceps*, for which the model with the highest Akaike weight corresponded to the non-linear fragmentation hypothesis (the model with the interaction term), and moderate support in 6 of 10 species (one of the 3 best-supported models is the interaction model). This result also agrees with several theoretical investigations, which have predicted non-linear fragmentation effects (Andrén, 1994b; Fahrig, 1998; With and King, 1999; Wiegand et al., 2005). Whether model results correspond either to the linear or non-linear fragmentation hypotheses, landscape fragmentation has a relatively strong effect, in comparison to forest area, in determining species presence. There is sufficient evidence for this conclusion in most species, from both the 10-best-supported models and all 30 models considered, and estimated area, fragmentation and interaction coefficients (Fig. 6, Appendix 1).

Evidence against or in favor of the non-linear fragmentation hypothesis, as Betts et al. (2006b, 2007) have stated, is as yet rare. More common are mixed results concerning the importance of fragmentation in determining species occurrence, as opposed to the sole importance of habitat area (McGarigal and McComb, 1995; Trczinski et al., 1999; Villard et al., 1999; Westphal et al., 2003; Betts et al., 2006b, 2007). More often, researchers find a much greater effect of habitat amount in determining species presence (Fahrig, 2002, 2003), although this is contested by Betts et al. (2006b). We agree with Betts and colleagues in that fragmentation effects are less critical than habitat area, but in our case play a much more important role than that found in northernmost latitudes.

R. sulphuratus and *P. montezuma* responded positively to landscape fragmentation (negative coherence coefficient), i.e., a higher probability of occurrence was predicted at higher levels of fragmentation, although they responded positively to proportion of forest cover. *R. sulphuratus* is relatively common in modified landscapes, being able to move easily between forest remnants using isolated, mature trees and hedgerows in open pastures (Stiles and Skutch, 1989; Cerezo et al., 2009; Graham, 2001a,b). Graham (2001a,b) studied factors influencing movement patterns and activity budgets of this species in fragmented landscapes in Southern Mexico. She discovered that remnant area was not influential in the sense that toucans did not preferentially move to large patches, and all activities (feeding, perching, social interactions, etc.) occurred in similar proportions in all habitat types, suggesting that different habitats provide many of the same resources. *P. montezuma* is a colony nester, usually nesting in isolated, large trees in clearings and forest edge (Stiles and Skutch, 1989). It also travels long distances for foraging in continuous forest from colony locations (Skutch, 1954). Thus, both species may have large a dispersal ability, can tolerate fragmented habitats and/or benefit from a moderate amount of fragmentation at adequate proportions of forest cover.

The Magnolia Warbler (*D. magnolia*) is a clear outlier in its response to both cover and fragmentation variables, and the scale of its response. This species is a migrant rather than a resident, and migrants are considered to have more general habitat requirements than residents, during migration and overwintering periods (Saab and Petit, 1992; Robbins et al., 1992). Also it is likely that many of the birds included in the study were actually on migration rather than on winter territory at the time they were observed. Finally, *D. magnolia* is not a deep forest bird, but is an edge specialist on its breeding grounds (Bent, 1953).

We found significant correlations between the AIC_c, AUC, and area coefficient, and species habitat breadth (Table 4). A very high and significant positive correlation between the AIC and habitat breadth reflects species' greater vulnerability to tropical forest modification at the landscape scale when their ability to use secondary habitats is reduced (and thus a better relative fit of a model with predictive variables related only to tropical forest). This is a very important result, since models are the mathematical formalizations of the ecological hypotheses being put forth: the AIC is thus a measure of how well the hypothesis fits the actual distribution of species in space, depending on the amount and degree of (area-dependent or independent) fragmentation. This result thus provides a clear link between a mechanistic ecological hypothesis regarding species responses to landscape modification and the statistical models constructed, a link which, according to Austin (2007), is infrequently addressed. In particular, this is also evidenced by a negative correlation between habitat breadth and the area coefficient: the species with a narrower habitat breadth have a stronger dependence on the proportion of forest cover (Table 4).

The hypothesis that species' tolerance of matrix habitats in the tropics enables them to survive better in fragmented tropical landscapes has been gaining more and more support from empirical data: results from BDFFP indicate that species with small area needs which tolerate matrix and edge habitats are the least vulnerable to habitat fragmentation (Stouffer and Bierregard, 1995; Gascon et al., 1999; Laurance et al., 2002), and in tropical Australia, the proneness of mammals to extinction appears to be inversely correlated to tolerance towards conditions in the prevailing matrix vegetation of the fragmented landscape (Laurance, 1991). As Sekercioglu (2007, p. 284) states: "mobility enables species to persist in fragments, so long as forest birds can use the surrounding matrix". Distance (from an occupied or unoccupied site) itself may not be a good proxy for isolation, since some forest birds will not cross even relatively small deforested zones (Bierregaard et al., 1992), and other studies have found cattle pastures and agricultural fields near absolute barriers for tropical forest birds (Stouffer and Bierregard, 1995; Laurance, 2004). Finally, with regard to habitat breadth and patch colonization ability, Ferraz et al. (2007) discovered that poor colonizers that rarely cross open areas should have relatively low equilibrium patch occupancy values in isolated patches.

Our final discussion deals with model use for inferential and practical (predictive) purposes. In terms of inference regarding the effects of area, fragmentation and their interaction, on species presence, our data indicates that for several species, models with greatest support include significant coherence and/or interaction terms. Nonetheless, this does not mean that these are the best models for predictive purposes. For those species for which the area model had the highest Akaike weight, but was strongly contested by area-coherence or interaction models, as in *M. momota*, *R. sulphuratus*, *H. decurtatus*, *T. maculipectus*, and *P. montezuma*, the area model still proved to have the highest ability in correctly discriminating presences from absences, according to the AUC (Table 3).

It is important to note that this phenomenon discussed in the previous paragraph only occurs when predictions were made using the cross-validation method. AUC values calculated using the traditional method (generating one model from all the data and obtaining AUC, sensitivity and specificity values from this model, see Appendix 2) systematically increased with model complexity. In other words, we discovered that the AUC values calculated from predictions from models of the same scale, using the full data set, behaved like the deviance or unadjusted R^2 values, in the sense that the more predictive variables the model had, the greater was its AUC value, or discrimination ability (note: the deviance has an inverse behavior: the more parameters in the model, the smaller the deviance), even when estimates of parameters where not significant. Consequently, using these values, calculated from predictions from models derived from the full data set, for comparing the discrimination ability of models of the same scale, did not seem like a sound practice, because full models will always present greater AUC values than models with predictive variables which are subsets of predictive variables of these full models.

Conversely, when AUC values were calculated from model predictions generated from cross-validation, these behaved similarly to the AIC values: those values most supported by the data had greater discrimination ability, independent of the number of parameters it contained. We thus strongly recommend cross-validation as an omnibus method for generating predictions, that will later be used to evaluate a model's discrimination ability (through the calculation of model's correctly and incorrectly predicted absences and presences, as well as its discrimination ability). Finally, it is important to add that this recommendation is valid in a model-selection or model-comparison context.

The AUC was also highly correlated with species' habitat breadth, which was an expected and desirable characteristic of models. Those species with a limited habitat breadth would probably be the species of conservation concern in fragmented landscapes, and a greater predictive capacity of models associated to these species will make them more powerful and useful conservation tools.

5. Conclusions

Our results indicate that bird response to landscape forest loss and fragmentation at the 1000-m scale was much stronger than at the 200- and 500-m scales. We thus conclude that the persistence of these species in fragmented landscapes depends on factors which operate beyond the territory scale, namely extra-territorial dispersal movements.

With regard to the relative importance of tropical forest area and fragmentation in determining species presence, forest area was generally more important than landscape fragmentation in explaining bird species occurrence, a result that agrees with previous studies. Nevertheless, there is also strong evidence of species responses to fragmentation. More importantly, we found strong evidence for an area-dependent fragmentation effect on bird species presence: species are affected by forest fragmentation, but effects are much stronger at lower levels of forest cover. These findings agree with several theoretical investigations, which have predicted non-linear fragmentation effects. These effects were in general much more pronounced in our study species than for bird species studied in North America and Australia.

We hypothesized that a species' ability to move through the matrix of a fragmented landscape depended on its habitat breadth. We predicted that those species with a greater dependency on tropical forest, i.e., that elicited a narrower habitat breadth, would be more affected by a reduction in forest area and an increase in fragmentation. In effect, we found relatively strong linear relationships among model statistics and coefficients and species' habitat breadth, lending support to this prediction. The number of secondary habitats used by a species was negatively associated with model AIC_c's, and the area and interaction coefficients, indicating that species with a narrower habitat breadth were more affected by landscape forest area, and by fragmentation at low levels of forest area. Models with a greater predictive ability also corresponded to species with a narrower habitat breadth, which is a desirable quality if these are to be used as conservation tools, since these species will probably be those of conservation concern in fragmented landscapes.

Acknowledgments

We would like to thank the National Fish and Wildlife Foundation, the Tennessee Chapter of the Nature Conservancy and the Foundation for Ecodevelopment and Conservation (FUNDAECO) for providing financial support. We also extend our gratitude to Teresa Boca, at the Institute of Climate and Water, National Institute of Agrarian Technology (Instituto de Clima y Agua, INTA-Castelar) of Argentina, for allowing us to perform statistical analyses with the SAS package at their facilities. Finally, we especially want to thank Barbara Dowell and Miguel Ramírez for their support in fieldwork activities, and four anonymous reviewers for important comments on earlier drafts of this work.

Appendix 1.

Akaike weights (w_i), parameter estimates and standard errors for all models shown in Table 3.

Species	w_i	Intercept	S.E.	Area	S.E.	Coherence	S.E.	Interaction	S.E.
P. nigrirostris	0.86	−2.48	0.97	2.57	1.43	1.86	1.04	16.82	7.86
	0.06	−2.66	1.25	3.39	1.73	2.59	1.07		
	0.03	−1.67	0.70			2.83	1.23		
T. melanocephalus	0.20	0.45	0.25			1.34	0.47		
	0.19	0.50	0.26			1.46	1.03		
	0.15	0.01	0.31	1.66	0.91				
M. momota	0.47	−2.84	0.49	5.78	1.04				
	0.30	−2.68	0.55	5.18	1.20	1.35	0.67		
	0.22	−2.70	0.54	5.42	1.28	0.79	0.87	8.07	4.80
R. sulphuratus	0.39	−2.96	0.64	5.97	1.52				
	0.37	−3.29	0.58	6.81	1.36	−1.91	0.84		
	0.16	−3.21	0.53	6.59	1.25	−1.53	0.95	−3.44	4.56
X. flavigaster	0.37	−1.84	0.63	2.84	1.19	1.90	0.95		
	0.25	−2.02	0.53	3.47	0.92				
	0.15	−1.82	0.61	2.80	1.17	1.81	1.00	2.99	6.35
H. decurtatus	0.52	−3.63	1.22	6.30	3.11				
	0.26	−3.61	1.22	6.22	3.07	0.62	0.93		
	0.19	−3.62	1.09	6.24	2.82	−0.56	1.10	9.11	4.17
T. maculipectus	0.40	−1.64	0.56	4.31	1.19				
	0.25	−1.88	0.48	5.03	1.02	−0.94	1.60	11.46	7.27
	0.17	−1.70	0.56	4.51	1.15	−0.49	1.13		
D. magnolia	0.28	−0.94	0.47	1.51	1.50				
	0.12	−0.78	0.53	0.76	1.52				
	0.10	−1.22	0.55	1.45	1.56	0.34	0.73		
S. atriceps	0.37	−0.75	0.41	2.47	0.97	0.82	0.99	14.68	5.87
	0.19	−0.76	0.36	2.37	0.74				
	0.11	−0.67	0.38	2.09	0.73	0.84	0.70		
P. montezuma	0.45	−0.78	0.42	3.50	2.21				
	0.25	−0.78	0.50	3.51	2.26	−0.21	0.79	−9.78	3.56
	0.16	−0.80	0.41	3.56	2.27	−0.16	0.80		

Appendix 2.

Model fit and selection statistics for all constructed models; AUC values were calculated from the full data set, not by cross-validation (see Section 4 for details); legend for parameter abbreviations: COHR, coherence; INT, interaction.

Species	Model	Scale	LRT p-value	HL p-value	$\#\beta$	Dev.	d.f.	AIC_c	w_i	AUC
Patagionenias nigrirostris	Area + COHR + INT	1000	<0.01	0.74	4	86.87	108	95.24	0.43	0.76
Short-billed Pigeon	Area + COHR	1000	<0.05	0.75	3	90.72	109	96.94	0.19	0.69
	Area	1000	0.08	0.05	2	93.63	110	97.74	0.12	0.67
	Area	500	0.43	0.04	2	94.36	110	98.47	0.09	0.67
	COHR	1000	0.05	0.09	2	95.82	110	99.93	0.04	0.65
	Area + COHR	500	0.08	0.73	3	93.76	109	99.98	0.04	0.67
	Area	200	0.09	0.42	2	95.96	110	100.07	0.04	0.48
	Area + COHR + INT	500	0.15	0.54	4	93.48	108	101.85	0.02	0.67
	Area + COHR	200	0.24	0.48	3	95.92	109	102.14	0.01	0.47
	COHR	500	0.45	0.31	2	98.19	110	102.30	0.01	0.53
	COHR	200	0.91	0.57	2	98.74	110	102.85	0.01	0.58
Trogon melanocephalus	COHR	500	0.19	0.36	2	147.39	110	151.50	0.25	0.57
Black-headed Trogon	Area	1000	0.14	0.13	2	147.93	110	152.04	0.19	0.59
	Area + COHR	500	0.33	0.96	3	147.11	109	153.33	0.10	0.60
	Area + COHR	1000	0.27	0.27	3	147.49	109	153.72	0.08	0.60
	COHR	1000	0.52	0.07	2	149.66	110	153.77	0.08	0.52
	Area	500	0.49	0.33	2	149.83	110	153.94	0.07	0.55
	COHR	200	0.64	0.09	2	149.86	110	153.97	0.07	0.50
	Area	200	0.81	0.56	2	150.02	110	154.13	0.07	0.53
	Area + COHR + INT	1000	0.32	0.01	4	146.56	108	154.94	0.04	0.61
	Area + COHR + INT	500	0.48	0.81	4	147.63	108	156.00	0.03	0.59
	Area + COHR	200	0.88	0.38	3	149.83	109	156.05	0.03	0.51
Momotus momota	Area	1000	<0.001	0.63	2	108.23	110	112.34	0.63	0.79
Blue-crowned Motmot	Area + COHR	1000	<0.001	0.96	3	107.97	109	114.19	0.25	0.79
	Area + COHR + INT	1000	<0.001	0.48	4	107.56	108	115.94	0.10	0.79
	Area	500	<0.001	0.68	2	116.44	110	120.55	0.01	0.72
	Area + COHR	500	<0.005	0.40	3	115.70	109	121.92	0.01	0.72
	Area + COHR + INT	500	<0.005	0.61	4	118.68	108	127.05	0.00	0.72
	Area + COHR	200	0.02	0.54	3	124.00	109	130.23	0.00	0.68
	Area	200	0.02	0.74	2	126.82	110	130.93	0.00	0.65
	COHR	200	0.23	0.03	2	130.71	110	134.82	0.00	0.50
	COHR	500	0.45	0.90	2	131.48	110	135.59	0.00	0.55
	COHR	1000	0.54	0.17	2	131.75	110	135.86	0.00	0.56
Ramphastos sulphuratus	Area + COHR	1000	<0.001	0.17	3	102.18	109	108.40	0.61	0.81
Keel-billed Toucan	Area + COHR + INT	1000	<0.001	0.14	4	102.07	108	110.44	0.22	0.82
	Area	1000	<0.001	0.02	2	107.24	110	111.35	0.14	0.78
	Area + COHR	200	<0.001	0.54	3	108.58	109	114.81	0.02	0.76
	Area + COHR	500	0.03	0.01	3	112.39	109	118.61	0.00	0.67
	Area	500	0.03	0.82	2	117.11	110	121.22	0.00	0.65
	COHR	200	<0.005	0.27	2	117.91	110	122.02	0.00	0.64
	Area	200	0.03	0.52	2	123.20	110	127.31	0.00	0.64
	COHR	500	0.13	0.25	2	123.89	110	128.00	0.00	0.58
	COHR	1000	0.07	0.02	2	124.83	110	128.94	0.00	0.61
	Area + COHR + INT	500	0.07	0.00	4	121.01	108	129.39	0.00	0.68
Xiphorhynchus flavigaster	Area + COHR	1000	<0.01	0.10	3	120.48	109	126.70	0.34	0.69
Ivory-billed Woodcreeper	Area	1000	<0.01	0.36	2	122.66	110	126.77	0.32	0.67
	Area + COHR + INT	1000	<0.05	0.46	4	120.44	108	128.81	0.12	0.69
	Area	500	0.05	0.75	2	125.16	110	129.27	0.09	0.63
	Area + COHR	500	0.10	0.19	3	124.72	109	130.94	0.04	0.63
	COHR	1000	0.14	0.16	2	127.99	110	132.10	0.02	0.58
	Area	200	0.15	0.63	2	128.06	110	132.17	0.02	0.60
	Area + COHR + INT	500	0.10	0.53	4	123.89	108	132.26	0.02	0.64
	COHR	500	0.40	0.22	2	129.77	110	133.88	0.01	0.53
	Area + COHR	200	0.34	0.35	3	128.01	109	134.23	0.01	0.59
	COHR	200	0.99	0.48	2	130.17	110	134.28	0.01	0.50
Hylophilus decurtatus	Area	1000	<0.001	0.72	2	83.76	110	87.87	0.57	0.78
Lesser Greenlet	Area + COHR	1000	<0.001	0.65	3	83.31	109	89.54	0.25	0.79
	Area + COHR + INT	1000	<0.001	0.87	4	82.30	108	90.67	0.14	0.80
	Area	500	<0.001	0.36	2	90.38	110	94.49	0.02	0.72
	Area + COHR	500	<0.005	0.30	3	89.64	109	95.86	0.01	0.73
	Area + COHR	200	<0.01	0.07	3	91.56	109	97.78	0.00	0.72
	Area + COHR + INT	500	<0.01	0.93	4	89.57	108	97.94	0.00	0.73
	Area	200	0.01	0.24	2	95.37	110	99.48	0.00	0.71
	COHR	200	0.20	0.12	2	100.34	110	104.45	0.00	0.55
	COHR	1000	0.39	0.09	2	101.25	110	105.36	0.00	0.59
	COHR	500	0.41	0.05	2	101.33	110	105.44	0.00	0.56

Species	Model	Scale	LRT p-value	HL p-value	$\#\beta$	Dev.	d.f.	AIC_c	w_i	AUC
Thryothorus maculipectus	Area	1000	<0.001	0.23	2	135.83	110	139.94	0.43	0.71
Spotted-breasted Wren	Area + COHR	1000	<0.001	0.56	3	134.96	109	141.18	0.23	0.72
	Area + COHR + INT	1000	<0.001	0.64	4	133.62	108	142.00	0.15	0.73
	Area + COHR	200	<0.005	0.12	3	136.90	109	143.12	0.09	0.70
	Area	500	<0.001	0.48	2	140.43	110	144.54	0.04	0.70
	Area + COHR + INT	500	<0.005	0.60	4	137.01	108	145.39	0.03	0.70
	Area + COHR	500	<0.005	0.48	3	140.28	109	146.51	0.02	0.70
	Area	200	0.01	0.12	2	143.59	110	147.70	0.01	0.66
	COHR	200	0.04	0.96	2	145.79	110	149.90	0.00	0.59
	COHR	1000	0.40	0.35	2	149.38	110	153.49	0.00	0.56
	COHR	500	0.99	0.72	2	149.98	110	154.09	0.00	0.50
Dendroica magnolia	Area	200	0.12	0.56	2	144.65	110	148.76	0.28	0.58
Magnolia Warbler	Area	500	0.46	0.70	2	146.32	110	150.43	0.12	0.55
	COHR	1000	0.45	0.85	2	146.56	110	150.67	0.11	0.54
	Area	1000	0.53	0.29	2	146.73	110	150.84	0.10	0.54
	Area + COHR	200	0.29	0.59	3	144.65	109	150.87	0.10	0.58
	COHR	500	0.77	0.58	2	147.07	110	151.18	0.08	0.50
	COHR	200	0.85	0.42	2	147.10	110	151.21	0.08	0.49
	Area + COHR	1000	0.61	0.21	3	146.15	109	152.38	0.05	0.56
	Area + COHR	500	0.73	0.63	3	146.26	109	152.48	0.04	0.54
	Area + COHR + INT	1000	0.52	0.11	4	144.85	108	153.23	0.03	0.59
	Area + COHR + INT	500	0.89	0.85	4	146.50	108	154.87	0.01	0.54
Saltator atriceps	Area + COHR + INT	1000	<0.05	0.70	4	143.91	108	152.28	0.45	0.67
Black-headed Saltator	Area	1000	<0.05	0.33	2	150.03	110	154.14	0.18	0.58
	Area	500	0.20	0.38	2	151.23	110	155.34	0.10	0.58
	Area + COHR	1000	0.06	0.43	3	149.19	109	155.41	0.09	0.63
	Area	200	0.23	0.97	2	153.25	110	157.36	0.04	0.56
	Area + COHR	500	0.44	0.38	3	151.18	109	157.40	0.03	0.59
	COHR	200	0.25	0.05	2	153.35	110	157.46	0.03	0.52
	Area + COHR	200	0.19	0.38	3	151.39	109	157.61	0.03	0.59
	COHR	1000	0.37	0.15	2	153.89	110	158.00	0.03	0.56
	COHR	500	0.99	0.50	2	154.65	110	158.76	0.02	0.50
	Area + COHR + INT	500	0.65	0.35	4	153.06	108	161.43	0.00	0.59
Psarocolius montezuma	Area	1000	<0.01	0.34	2	144.29	110	148.40	0.48	0.68
Montezuma Oropendola	Area + COHR	1000	<0.01	0.32	3	143.73	109	149.95	0.22	0.69
	Area + COHR + INT	1000	<0.01	0.58	4	142.35	108	150.73	0.15	0.70
	Area	500	0.01	0.17	2	147.81	110	151.92	0.08	0.65
	Area + COHR	500	0.04	0.38	3	147.60	109	153.82	0.03	0.66
	Area + COHR + INT	500	0.08	0.31	4	147.98	108	156.36	0.01	0.66
	Area	200	0.21	0.48	2	153.13	110	157.24	0.01	0.57
	COHR	1000	0.46	0.02	2	154.14	110	158.25	0.00	0.57
	COHR	500	0.57	0.75	2	154.53	110	158.64	0.00	0.48
	COHR	200	0.97	0.10	2	154.69	110	158.80	0.00	0.47
	Area + COHR	200	0.45	0.39	3	153.08	109	159.30	0.00	0.56

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