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Environmental suitability of a highly fragmented and heterogeneous landscape for forest bird species in south-eastern Brazil

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SUMMARY

Assessment of the suitability of anthropogenic landscapes for wildlife species is crucial for setting priorities for biodiversity conservation. This study aimed to analyse the environmental suitability of a highly fragmented region of the Brazilian Atlantic Forest, one of the world's 25 recognized biodiversity hotspots, for forest bird species. Eight forest bird species were selected for the analyses, based on point counts ($n = 122$) conducted in April–September 2006 and January–March 2009. Six additional variables (landscape diversity, distance from forest and streams, aspect, elevation and slope) were modelled in Maxent for (1) actual and (2) simulated land cover, based on the forest expansion required by existing Brazilian forest legislation. Models were evaluated by bootstrap or jackknife methods and their performance was assessed by AUC, omission error, binomial probability or p value. All predictive models were statistically significant, with high AUC values and low omission errors. A small proportion of the actual landscape (24.41 ± 6.31%) was suitable for forest bird species. The simulated landscapes lead to an increase of *c.*30% in total suitable areas. In average, models predicted a small increase (23.69 ± 6.95%) in the area of suitable native forest for bird species. Being close to forest increased the environmental suitability of landscapes for all bird species; landscape diversity was also a significant factor for some species. In conclusion, this study demonstrates that species distribution modelling (SDM) successfully predicted bird distribution across a heterogeneous landscape at fine spatial resolution, as all models were biologically relevant and statistically significant. The use of landscape variables as predictors contributed significantly to the results, particularly for species distributions over small extents and at fine scales. This is the first study to evaluate the environmental suitability of the remaining Brazilian Atlantic Forest for bird species in an agricultural landscape, and provides important additional data for regional environmental planning.

Keywords: agricultural landscape, Atlantic Forest, birds, Brazil, matrix heterogeneity, maximum entropy method (Maxent), species distribution modelling

INTRODUCTION

The Atlantic Forest, one of the most important biodiversity hotspots in the world (Mittermeier *et al.* 1999), has suffered dramatic and rapid changes due to habitat loss and fragmentation, with the most intensive disturbance levels occurring in south-eastern Brazil (Dean 1997; SOS Mata Atlântica & INPE [Instituto Nacional de Pesquisas Espaciais] 2008; Tabarelli *et al.* 2010). The unplanned expansion of both agricultural frontiers and urban areas has transformed the Atlantic Forest into agroecosystems with a patchwork of disconnected and disturbed forest remnants (SOS Mata Atlântica & INPE 2008), corresponding to < 16% of the original forest cover, with only 7.1% of the area being interior forest (SOS Mata Atlântica & INPE 2008; Ribeiro *et al.* 2009). The Corumbataí river basin, located in one of the most developed regions of São Paulo State (south-eastern Brazil), is a typical example of these landscape modifications, containing small (67.8% of the forest remnants in the Corumbatai river basin are < 1ha and only 0.7% are > 80ha), scattered and isolated remnants of original Atlantic Forest, with a distance of up to 1.47 km between fragments of < 5 ha, surrounded mainly by a matrix of sugar cane and pasture (Rodrigues 1999; Valente & Vettorazzi 2003, 2005). One of the main consequences of this fragmentation and habitat destruction is the precarious situation facing most of the endemic birds (Parker *et al.* 1996; Goerck 1997), with 98 of 160 endangered bird species occurring mainly in the Atlantic Forest (Silveira & Straube 2008).

Many studies consider the effects of landscape or habitat fragmentation on biodiversity (Turner 1996; Chiarello 1999; Lynam & Billick 1999; Laurance *et al.* 2002; Fahrig 2003), but few consider the influence of matrix heterogeneity (Devictor & Jiguet 2007; Umetsu *et al.* 2008; Prevedello & Vieira 2010). The matrix (the land cover type dominating others in area and connectivity; Forman & Godron 1986; Forman 1995; Metzger 2001), often a heterogeneous mosaic of different land cover types surrounding modified fragments in a human-dominated landscape, may exert a strong influence on vertebrate communities (Gascon *et al.* 1999; Laurance *et al.* 2002;

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Tischendorf *et al.* 2003; Uezu *et al.* 2005; Debinski 2006; Devictor & Jiguet 2007; Umetsu & Pardini 2007; Umetsu *et al.* 2008; Hansbauer *et al.* 2010; Prevedello & Vieira 2010). The ability of species to use the matrix (Antongiovanni & Metzger 2005; Uezu *et al.* 2008), the type of matrix (Prevedello & Vieira 2010) and the matrix quality (Vandermeer & Carvajal 2001; Umetsu & Pardini 2007; Umetsu *et al.* 2008) can be extremely important in determining the structure and persistence of vertebrate communities in heterogeneous and fragmented landscapes.

Forest specialist species are among the taxa most vulnerable to the conversion of forest into agriculture landscapes, as most struggle to exist in small and isolated forest remnants (Giraudo *et al.* 2008; Martensen *et al.* 2008; Boscolo & Metzger 2011). While some species may be restricted to the remaining forest fragments, others may be able to survive in different anthropogenic habitat types to various degrees (Hansbauer *et al.* 2010). The reduction and isolation of habitat patches can lead to a local loss of forest-dependent species, favouring habitat generalists (Willis 1979; Turner 1996; Stratford & Stouffer 1999; Willis & Oniki 2002; Antunes 2005; Giraudo *et al.* 2008). The dispersal capacity of some bird species between isolated patches can be limiting (Moore *et al.* 2008; Boscolo & Metzger 2011), especially in a landscape with a consolidated matrix (>40 years old), as the case in the Corumbataí river basin. Improving matrix connectivity and the potential for species dispersal within this landscape should be prioritized in conservation and environmental planning; habitat area has been considered an important predictor of bird species occurrence (Cerezo *et al.* 2010; Mortelliti *et al.* 2010, Smith *et al.* 2011).

Considering the importance of knowing the impacts of anthropogenic landscapes on vertebrate communities, this study aimed to evaluate the environmental suitability of a highly fragmented agricultural landscape in the Atlantic Forest (south-eastern Brazil) for forest-dependent bird species using species distribution modelling (SDM) techniques. SDM was also used to evaluate a simulated scenario assuming the expansion of forest remnants along all riparian zones (such as the buffer strips surrounding rivers and streams) on private landholdings, improving landscape connectivity for species distribution and dispersal, as required by current Brazilian forest legislation (Código Florestal 2001). This is particularly important, as Brazil risks suffering its worst environmental setback in half a century (Metzger *et al.* 2010), with the ongoing reform of its forest legislation (Brazilian Forest Act) condemning old-growth remnants and forest regrowth in private landholdings, potentially leading to irreversible loss of tropical biodiversity (Michalski *et al.* 2010).

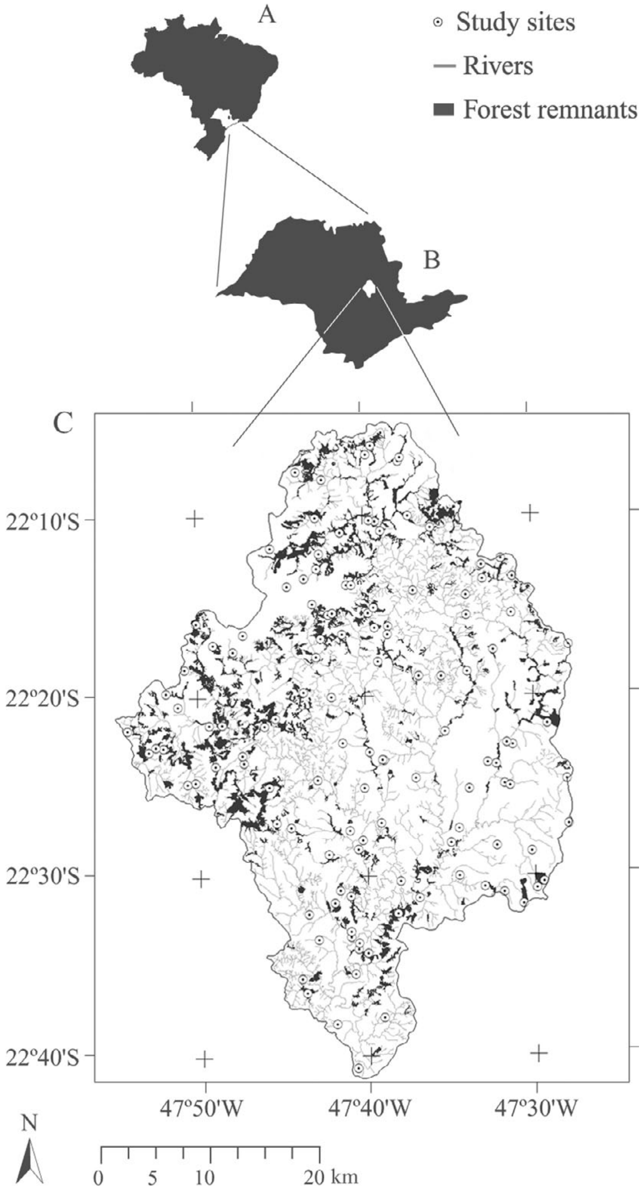

Figure 1 Location of the Corumbataí river basin (C) in São Paulo State (B), Brazil (A). Forest remnants and study sites are indicated (C).

METHODS

Study area

We undertook the study in the Corumbataí river basin (1710 km^2), in São Paulo state (22°04′–23°41′S, 47°26′–47°56′W; Fig. 1). The study area comprises eight municipalities, containing *c.* 530 000 inhabitants. The topography of the region is moderately undulating. The most important river is the Corumbataí river, which originates in the cuesta zone (1058 m at the headwaters), reaching the Piracicaba river (470 m at the discharge) after crossing Rio Claro city, the most important municipality in the basin (Garcia *et al.* 2006).

The study area is characterized by a landscape composed of sparse and scarce Atlantic Forest fragments surrounded by a matrix of sugar cane or pasture. After intensive and persistent anthropogenic landscape modifications, *c.*12% of original Atlantic Forest remains in the river basin in highly fragmented condition; most remnants follow the drainage network (Valente & Vettorazzi 2003). The landscape

Table 1 Characteristics of forest bird species used in models. Sensitivity to human disturbance obtained from Parker *et al.* (1996), biomes obtained from Parker *et al.* (1996), Sick (1997) and Sigrist (2006). *Endemic species from Atlantic Forest (according to Parker *et al.* 1996). **With occurrence in secondary forest.

Bird by order or family	*Sensitivity to human disturbance*	*Biomes*
Columbiformes		
Columbidae		
*Leptotila verreauxi***	Low	Atlantic Forest, Brazilian savannahs
Piciformes		
Picidae		
Picumnus albosquamatus	Low	Atlantic Forest, Brazilian savannahs
Passeriformes		
Thamnophilidae		
Thamnophilus caerulescens	Low	Atlantic Forest
Furnariidae		
*Automolus leucophthalmus**	Medium	Atlantic Forest
*Synallaxis spixi***	Low	Atlantic Forest, Brazilian savannahs
Tyrannidae		
Platyrinchus mystaceus	Medium	Atlantic Forest
Parulidae		
*Basileuterus flaveolus***	Medium	Atlantic Forest, Brazilian savannahs
Basileuterus hypoleucus	Low	Atlantic Forest

is a heterogeneous mosaic encompassing mixed cultivated fields, urban areas, pasture, forest remnants and eucalyptus plantations. Sugar cane (*c.* 26%) and pasture (*c.* 44%) are now the dominant land uses in the Corumbataí river basin (Valente & Vettorazzi 2003; Fig. 2).

Bird survey

We selected 122 study sites for bird surveys at random in order to spatially cover the river basin (Fig. 1). Study sites encompassed native forest (fragments and corridors), eucalyptus forest, pasture, sugar cane, perennial crops and urban areas. The same observer recorded all bird species that were seen or heard throughout the study. As we only used presence records, we surveyed birds using unlimited radius point counts (Ralph *et al.* 1995) during 20 min. in the early morning, April–September 2006 and January–March 2009. Sampling effort was the same for all sampling sites.

From the total 169 recorded species, for our model, we preferentially selected eight forest-dependent bird species (Sick 1997; Willis & Oniki 2003; Sigrist 2006; Table 1) for which we had recorded a reasonable number of observations. Species more vulnerable to fragmentation, such as *Odontophorus capueira*, *Hypoedaleus guttatus*, *Drymophila ferruginea* and *Pyriglena leucoptera* did not provide suitable sample sizes for modelling. Despite their low to medium sensitivity to human disturbances, the species analysed are considered forest-dependent, and we had previously established that their populations were suffering from the impacts of habitat loss and fragmentation. Thus, these eight species should act as appropriate indicators of the environmental suitability of the anthropogenic landscape for forest-dependent species.

Table 2 Description of landscape predictors used in the modelling.

Landscape predictors	*Description*
Landscape diversity	Landscape diversity by Shannon's landscape diversity index (Turner & Gardner 1991) quantified by an interpolated grid according to the inverse of distance weight (IDW) of systematic points 250 m distant from each other (Ferraz *et al.* 2010)
Distance from forest	Gradient distance in metres from forest fragment
Distance from streams	Gradient distance in metres from the closest main stream
Aspect	The direction that slopes face
Elevation	Elevation in metres
Slope	Terrain slope, expressed as a percentage

Modelling procedures

We used the species presence records and six landscape predictors with a spatial resolution of 20 m (Table 2) as our variables in the SDM. We produced two predictions for the potential species distributions. One set was modelled on the actual landscape, based on a 2003 land use/land cover map (Valente & Vettorazzi 2003; Fig. 2). The other set was modelled for a future simulated landscape, assuming that forest remnant areas had increased in compliance with current Brazilian forest legislation, requiring the set-aside of all riparian forest buffer strips along rivers and streams as a 'Permanent Protection Area' (Código Florestal 2001; Fig. 2). For the present study, we assumed this simulated landscape to contain forest buffer strips of 30 m width for any river or stream <10 m wide, and 50 m width for rivers and streams between 10 and 50 m wide. The consequent simulated land cover map assumed a 48% increase in forest corridors in the river basin, connecting fragmented forest cover over the whole drainage network. Landscape diversity and distance from the nearest forest fragment were calculated for both the actual and simulated land cover maps, and used for each model.

We used Maxent for our SDMs (see URL http://www.cs.princeton.edu/~schapire/maxent/; Phillips *et al.* 2004, 2006, 2009; Phillips & Dudík 2008). Maxent is a modelling technique that achieves high predictive accuracy. In maximum entropy density estimation, the true distribution of a species is represented as a probability distribution over the set of sites in the study area. This probability assigns a non-negative value to every site in the study area and respects a set of constraints derived from the occurrence data. The

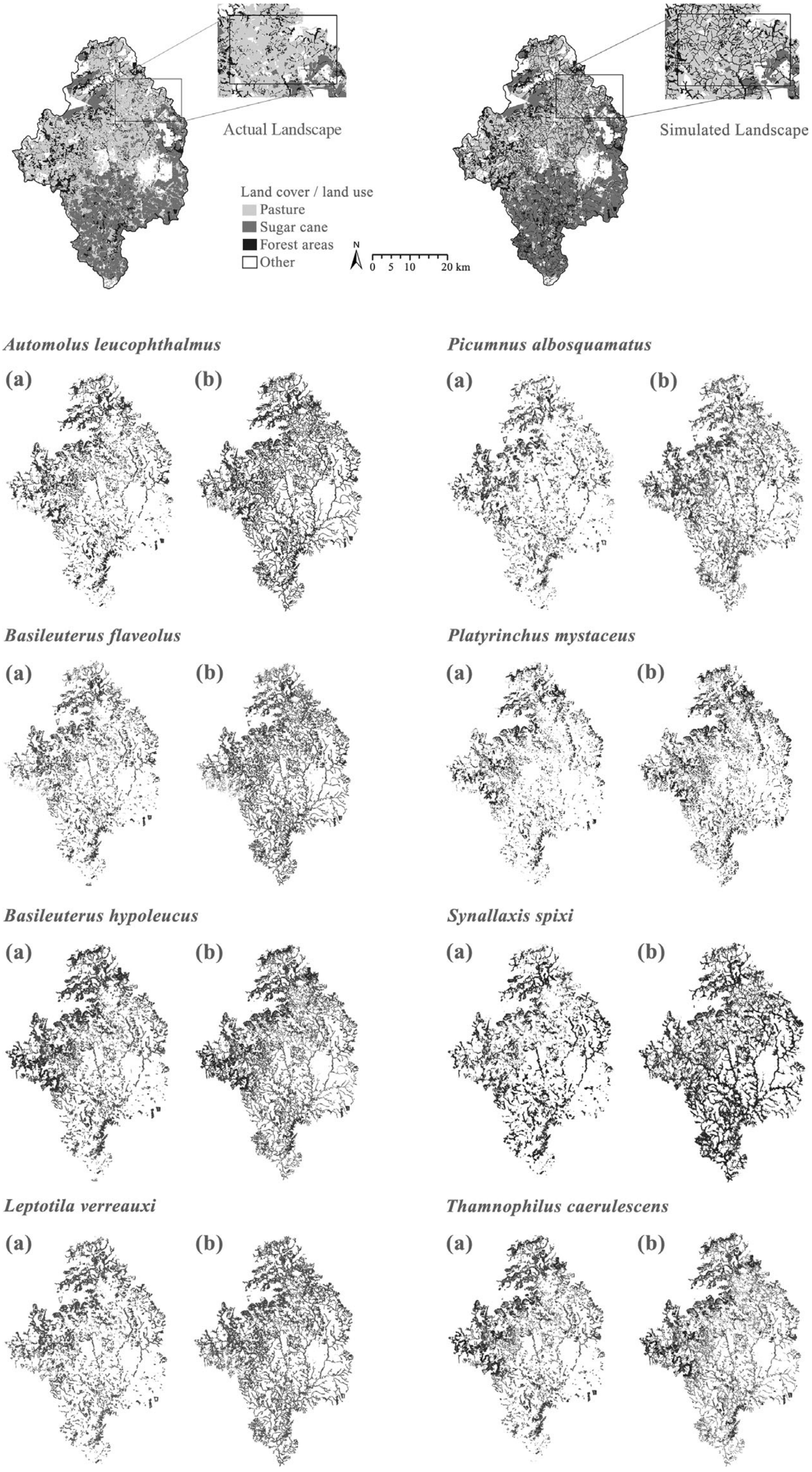

Figure 2 Land use / land cover map and environmental suitability models for eight forest bird species, as modelled for both (*a*) actual and (*b*) simulated landscapes (assuming riverine forest corridors in compliance with the mandatory permanent protection area required by Brazilian Federal Law).

Table 3 Total suitable area (km^2), suitable native forest (km^2) and increment (%) in suitable areas for forest bird species in both actual and simulated landscapes.

Bird species	*Total suitable area (km^2)*		*Increment (%)*	*Suitable native forest (km^2)*		*Increment (%)*
	Actual	*Simulated*		*Actual*	*Simulated*	
Automolus leucophthalmus	332.64	495.51	48.97	240.16	321.85	34.01
Basileuterus flaveolus	397.44	569.20	43.22	244.01	313.54	28.50
Basileuterus hypoleucus	578.88	578.61	−0.05	267.37	315.65	18.06
Leptotila verreauxi	442.92	626.66	41.49	245.51	299.93	22.17
Picumnus albosquamatus	350.43	495.16	41.30	172.48	218.95	26.94
Platyrinchus mystaceus	264.68	353.24	33.46	153.86	187.13	21.63
Synallaxis spixi	399.25	600.92	50.52	211.87	268.68	26.81
Thamnophilus caerulescens	552.21	521.53	−5.56	262.02	291.99	11.44

constraints are expressed in terms of simple functions of the environmental variables (features). Specifically, the mean of each feature must be close to the empirical average over the presence sites (Phillips & Dudík 2008).

Our model parameters were: a convergence threshold of 10^{-5} with 500 iterations and with 10 000 background points, auto features, and analysis of variable importance measured by jackknife, response curves and random seed. We defined two different partitioning methods, depending on the number of presence records of each species. We sampled datasets having at least 15 presence records by bootstrapping with 10 random replicates with replacement setting 70% of the dataset for training and 30% for testing models (Pearson 2007). Datasets with less than 15 presence points were sampled by a jackknife (or 'leave-one-out') procedure, where each observed locality was removed once from the set of data and we constructed the model using the remaining ($n - 1$) localities (Pearson *et al.* 2007). We assessed the predictive performance of each model on their ability to predict the single locality excluded from the training data set.

The logistic output format was used, which results in each grid cell in the map having values ranging continuously from 0 (least suitable) to 1 (most suitable). These values can be interpreted as indicating the environmental suitability for the target species (Phillips *et al.* 2004; Veloz 2009). We made the distinction between suitable and unsuitable areas, necessary for model validation and interpretation, by setting the 'maximum test sensitivity plus specificity' as a decision threshold rule. Sensitivity (Se) and specificity (Sp) are conditional probabilities widely used in SDM. Se is the probability that the model correctly predicts an observation of a species at a site, and Sp is the probability that a known absence site is correctly predicted (Liu *et al.* 2011). Both measures can be used to assess the overall prediction success of SDMs. The sum of Se and Sp can be maximized to give a better threshold (Manel *et al.* 2001; Liu *et al.* 2005), which is equivalent to finding a point on the receiver operating characteristic (ROC) curve whose tangent slope is equal to 1 (Cantor *et al.* 1999); the ROC curve characterizes the performance of a model under all possible thresholds, and is used to identify those areas with highest suitability (where the sum of Se and Sp is maximized), reducing the risk of choosing unsuitable sites for species (Pearce & Ferrier 2000).

The final model chosen was that based on the average produced by Maxent software (version 3.3.3e), which presented the mean value for each pixel based on the suitability values, for each of the 10 replicates used. We evaluated the models by calculating the area under the curve (AUC), a threshold-independent measure of overall model performance (Fielding & Bell 1997); the AUC is the probability that a randomly chosen presence site will be ranked above a random site, where a random ranking has, on average, an AUC of 0.5, and a perfect ranking achieves the best possible AUC of 1.0, although, when true presences and random points are used to calculate AUC, its maximum value is always <1. SDMs were evaluated by the omission error (false negative predictions) (Fielding & Bell 1997). We evaluated the significance of models generated by the bootstrapping method by the one-tailed binomial test (Anderson *et al.* 2003), and models generated with the jackknife procedure by a p value (Pearson *et al.* 2007).

RESULTS

Potential distribution areas for forest bird species were concentrated at and close to forest remnants (Fig. 2). The SDMs predicted an average of 24.41 ± 6.31% of the anthropogenic landscape as suitable for forest birds. These areas encompassed forest remnants (fragments and corridors), pasture and a small portion of sugar cane. Highly suitable areas ($\geq$0.7 suitability) represented no more than 2% of the area (ranging from 0 to 1.81%), encompassing only small portions of forest remnants for most species.

Simulated landscapes resulted in a low increase in the availability of total suitable areas for most of the species (averaging 43.16 ± 6.14%), except for *Thamnophilus caerulescens* and *Basileuterus hypoleucus*, and also in the area of suitable native forest (averaging 23.69 ± 6.95%) (Table 3).

All predictive models were statistically significant, with high AUC values and low omission errors (Table 4).

Table 4 AUC scores, test and training omission, binomial probability (based on bootstrapping method presented by Anderson *et al.* 2003) and *p* values (based on jackknife technique presented by Pearson *et al.* 2007). Threshold: maximum test sensitivity plus specificity. – = no value.

Species	*n*	*AUC test*	*Omission training*	*Omission test*	*Binomial probability*	*Success (%)*	*p value*
Automolus leucophthalmus	11	0.836	0.327	0	–	100	0
Basileuterus flaveolus	26	0.867 ± 0.042	0.121	0.029	0.003	–	–
Basileuterus hypoleucus	35	0.811 ± 0.050	0.116	0.110	0.000	–	–
Leptotila verreauxi	25	0.853 ± 0.054	0.050	0.057	0.001	–	–
Picumnus albosquamatus	28	0.807 ± 0.070	0.095	0.138	0.008	–	–
Platyrinchus mystaceus	9	0.830	0.361	0	–	100	0
Synallaxis spixi	14	0.757	0.330	0	–	100	0
Thamnophilus caerulescens	32	0.818 ± 0.048	0.052	0.044	0.002	–	–

Table 5 Per cent contribution of main landscape predictors to forest species models.

Species	*Variable contribution (%)*	
	Distance from forest	*Landscape diversity*
Automolus leucophthalmus	98.72	
Basileuterus flaveolus	67.89	
Basileuterus hypoleucus	72.20	
Leptotila verreauxi	62.98	15.02
Picumnus albosquamatus	55.72	22.75
Platyrinchus mystaceus	75.22	
Synallaxis spixi	61.25	32.17
Thamnophilus caerulescens	73.01	

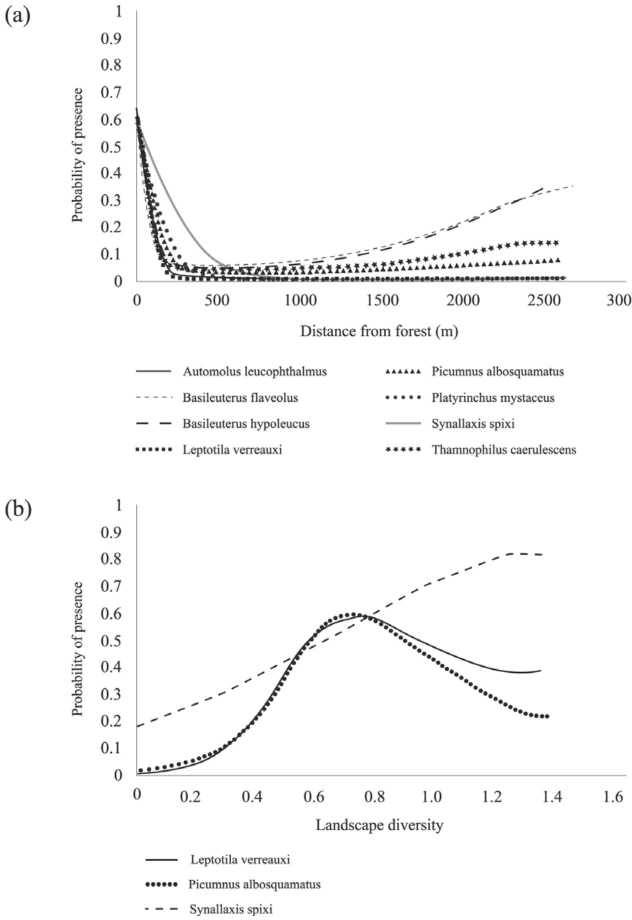

Figure 3 Logistic regression curves for the probability of occurrence against main landscape descriptors: (*a*) distance from forest and (*b*) landscape diversity for forest bird species.

Distance from forest was the highest contributor variable for all model predictions, although landscape diversity also explained the predicted distributions of *Leptotila verreauxi*, *Picumnus albosquamatus* and *Synallaxis spixi* (Table 5). In general, environmental suitability decreased as distance from fragments increased, and increased as landscape diversity increased (Fig. 3).

DISCUSSION

SDMs revealed the agricultural and fragmented landscape was only of low suitability for forest bird species in both current and simulated landscapes. As found across the entire Atlantic Forest region (Ribeiro *et al.* 2009), the Corumbataí river basin, one of the most developed regions in south-eastern Brazil (Garcia *et al.* 2006), is at a critical stage of the fragmentation process, with only *c.* 12% of the original Atlantic Forest remaining, represented by small and isolated forest fragments. More than 90% of remaining fragments in the river basin cover <5 ha (Valente & Vettorazzi 2005). Thus, the availability of suitable 'natural' habitats for forest species in the region is restricted (as for most of the Atlantic Forest in Brazil), as confirmed by our SDMs. Although the species modelled present medium to low sensitivity to human disturbance (Parker *et al.* 1996), the areas of their potential distributions were small, reflecting the restricted availability of suitable habitat in the river basin.

The SDMs revealed that suitable areas included most of the forest remnants and also a small portion of the surrounding agricultural matrix. Thus, the increase in total suitability for most of species (averaging 43.16%) generally resulted from an increase in pasture and sugar cane area considered as suitable in the final models, excluding *Basileuterus hypoleucus* and *Thamnophilus caerulescens*. However, as all species are forest dependent (Sick 1997; Willis & Oniki 2003; Sigrist

2006), they may not actually occur in matrix habitats such as sugar cane and pasture. This apparent suitability of the agricultural matrix may be an artefact of commission errors resulting from presence points located at the fragment edge being characterized as sugar cane or pasture when the location database was overlaid with the land cover maps.

The simulated land cover model assumed linear forest remnants (forest corridors) were distributed along the drainage network, as required by Brazilian federal law (Código Florestal 2001), predicting a small increase in suitable native forest (average of 23.69%; Table 3) for forest bird species occurrence. Narrow riparian forest corridors are a predominant feature of many deforested landscapes in Brazil, as current forest legislation requires that (1) all riparian zones on private landholdings are maintained as permanent reserves, and (2) riparian forest buffers fixed minimum width are retained alongside rivers and perennial streams (Lees & Peres 2008). Maintaining suitable corridor widths is crucial for biodiversity conservation, as the effects of fragmentation are striking within 100 m of forest edges (Laurance *et al.* 2002), and narrow remnant corridors may therefore fail to provide suitable habitat for many forest vertebrate species, retaining only a relatively depauperate vertebrate assemblage typical of deforested habitats (Lees & Peres 2008).

Most of the riparian forest corridors in south-eastern Brazil are narrow remnant riparian buffers set aside following deforestation; these are typically highly degraded and of low conservation value. As tropical landscapes become increasingly human-dominated, deforested and fragmented, riparian corridors are becoming disproportionately important in connecting and harbouring populations of tropical forest organisms (Sekercioglu 2009). A revision of the Brazilian Forest Act, the main Brazilian environmental legislation for privately-owned land, proposes reductions in the area of forest that must be retained along rivers and streams, and is currently awaiting approval by Congress (Metzger *et al.* 2010). If approved, this revision could lead to an irreversible loss of tropical biodiversity (Michalski *et al.* 2010), aggravating the critical situation facing the conservation of biodiversity in Atlantic Forest remnants.

Distance from forest was the most critical variable in our model predictions. We used this continuous variable in place of the corresponding categorical land cover variable to avoid an increase in the number of variables required in our models. Landscape diversity, distance from streams, slope and aspect were also important in predicting the potential distribution of some species, suggesting that the distribution patterns for the forest-dependent species (excluding *Automolus leucophthalmus*) occurring in this agricultural landscape depended on other environmental descriptors besides the extent of forest cover. Proximity to forest fragments and landscape diversity (heterogeneity) increased environmental suitability for all forest bird species.

Heterogeneity and extent of habitat cover are often positively correlated with the richness of taxonomic assemblages (Radford *et al.* 2005; Bennett *et al.* 2006; Devictor & Jiguet 2007; Haslem & Bennett 2008), while the composition of the habitat mosaic (based on the proportions of elements present) is associated with the species composition (Bennett *et al.* 2006). However, the role of heterogeneity in species distribution patterns, especially in modified and heterogeneous landscapes, still remains unclear. The results of this study highlighted the importance of quantifying and including landscape variables as descriptors in modelling species distributions.

The heterogeneous mosaic of the agricultural landscape in south-eastern Brazil could be related to the amount of available critical resources and surrounding habitats for the local biodiversity. According to Kennedy *et al.* (2010), the structure, composition and land-use disturbance regimes in matrix areas have an overall impact on the habitat quality in landscapes by potentially mediating resource availability inside as well as outside of forest habitats. The population's persistence for many species in agriculturally dominated landscapes depends not only on the amount of surrounding habitats, but also on the existence of favourable habitats within the adjacent matrix (Devictor & Jiguet 2007).

CONCLUSIONS

The SDM proved to be an efficient tool for modelling species distributions in a small region with a fine spatial resolution, as all models were biologically relevant and statistically significant, with high AUC scores and low omission errors. Spatial scale can play an important role in the application of species' distribution models (Pearson 2007). In general, SDMs have been used at continental scales, using datasets that cover large extents with a coarse resolution. Ideally, as pointed out by Pearson (2007), the data resolution should be relevant to (1) the species under consideration, (2) the study question and (3) the desired application.

The use of landscape structure variables in the SDMs contributed significantly to the accuracy of our species distribution predictions. Most SDMs are generated using environmental data, which describe the region where the species occur, represented by climate and topographical variables (see Pearson 2007); landscape structure variables have been used relatively rarely. The incorporation of landscape variables is strongly encouraged for future similar studies; they may better explain habitat suitability, and are particularly critical for species distributions over small extents and at fine scales.

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