ORIGINAL ARTICLE

Assessing the impact of deforestation and climate change on the range size and environmental niche of bird species in the Atlantic forests, Brazil

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ABSTRACT

Aim Habitat loss and climate change are two major drivers of biological diversity. Here we quantify how deforestation has already changed, and how future climate scenarios may change, environmental conditions within the highly disturbed Atlantic forests of Brazil. We also examine how environmental conditions have been altered within the range of selected bird species.

Location Atlantic forests of south-eastern Brazil.

Methods The historical distribution of 21 bird species was estimated using MAXENT. After superimposing the present-day forest cover, we examined the environmental niches hypothesized to be occupied by these birds pre- and post-deforestation using environmental niche factor analysis (ENFA). ENFA was also used to compare conditions in the entire Atlantic forest ecosystem pre- and post-deforestation. The relative influence of land use and climate change on environmental conditions was examined using analysis of similarity and principal components analysis.

Results Deforestation in the region has resulted in a decrease in suitable habitat of between 78% and 93% for the Atlantic forest birds included here. Further, Atlantic forest birds today experience generally wetter and less seasonal forest environments than they did historically. Models of future environmental conditions within forest remnants suggest generally warmer conditions and lower annual variation in rainfall due to greater precipitation in the driest quarter of the year. We found that deforestation resulted in a greater divergence of environmental conditions within Atlantic forests than that predicted by climate change.

Main conclusions The changes in environmental conditions that have occurred with large-scale deforestation suggest that selective regimes may have shifted and, as a consequence, spatial patterns of intra-specific variation in morphology, behaviour and genes have probably been altered. Although the observed shifts in available environmental conditions resulting from deforestation are greater than those predicted by climate change, the latter will result in novel environments that exceed temperatures in any present-day climates and may lead to biotic attrition unless organisms can adapt to these warmer conditions. Conserving intra-specific diversity over the long term will require considering both how changes in the recent past have influenced contemporary populations and the impact of future environmental change.

Keywords
Atlantic forest, biodiversity surrogates, birds, Brazil, climate change, conservation, deforestation, ecological niche modelling, environmental space, species distribution modelling.

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INTRODUCTION

Assessing the impacts of habitat loss and climate change on species is critical for understanding the persistence of species over the long term. For species with small geographic range sizes in particular, as is the case with many endemic species, habitat loss is a major factor influencing population declines and vulnerability to extinction (e.g. Davies *et al.*, 2009). In the past, climate change has been hypothesized as a major driver of species extinctions, and future climate change is likely to be an increasing threat to many species, especially those in higher latitudes and elevations (Millennium Ecosystem Assessment, 2005). Similar to habitat loss, future climate changes are often predicted to result in a reduction of suitable habitat within a species' current range extent (Thuiller *et al.*, 2006; Şekercioğlu *et al.*, 2008) and, in some cases, persistence will be dependent on the ability to disperse over landscape elements that present significant barriers (Colwell *et al.*, 2008). This assumes that species will not be able to adapt to new environmental conditions, either because of lack of evolutionary potential to do so or because of insufficient time.

The impact of deforestation on species is generally quantified in terms of the patterns and amount of habitat loss, fragmentation, edge effects and reduction of landscape connectivity (e.g. Harris & Pimm, 2004, 2008; Ferraz *et al.*, 2005; Martensen *et al.*, 2008; Boscolo & Metzger, 2009). From a geographic perspective, deforestation results in less habitat being available for forest species, thus reducing overall population sizes (e.g. Andrén, 1994; Burke & Nol, 2000). Deforestation also frequently creates landscapes with lowered connectivity of forest patches which, depending on the dispersal characteristics of species, may affect populations through lowered dispersal success and changes in species composition (e.g. Fahrig & Merriam, 1985; Uezu *et al.*, 2005). Moreover, changes in dispersal dynamics and movement pattern may influence the genetic structure of populations across a region (e.g. Veit *et al.*, 2005; Dixo *et al.*, 2008).

Relatively little attention has been given to how geographic changes associated with habitat loss might influence the range of environments or habitats (environmental diversity) across a species' range. Likewise, those climate change studies predicting range shifts and shrinkage (e.g. Lenoir *et al.*, 2008; Moritz *et al.*, 2008) rarely quantify the loss of environmental diversity and the shift in environmental conditions within species ranges. Understanding the impact of habitat loss and future climate change on environmental conditions within a species' range, especially when significant physical barriers constrain dispersal, is important for conservation of biological diversity because intra-specific variation in behavioural, physiological, morphological and genetic diversity is often linked to different types of environments (e.g. Calsbeek *et al.*, 2006; Thomassen *et al.*, 2009).

Deforestation is likely to result in non-random change in environmental diversity within the range of a species; such environmental changes can be expected to lead to further loss of morphological, behavioural and, often, cryptic genetic diversity (Wright *et al.*, 2006). For example, Rissler & Apodaca (2007) demonstrated that genetic divergence was associated with divergence in environmental parameters in the salamander *Aneides flavipunctatus*. Similarly, Dixo *et al.* (2008) found that genetic diversity of an endemic toad (*Rhinella ornata*) from the Atlantic forests in Brazil is higher in larger, more environmentally heterogeneous patches. Both of these studies highlight the importance of considering the range of environmental conditions in which a species exists when assessing the influence of habitat loss and fragmentation for any given species. Deforestation may also limit future success in tracking environmental conditions under conditions of climate change due to the need to disperse over unsuitable habitat (Colwell *et al.*, 2008; Hoegh-Guldberg *et al.*, 2008). Reduction in intra-specific diversity also may have long-term impacts on a species' ability to adapt to future environmental change (e.g. global warming; Willi *et al.*, 2006). Given that limited resources and time prevent exhaustive efforts to measure genetic, morphological and behavioural diversity for most species, efforts should be directed to conserve surrogates of this diversity (Margules & Pressey, 2000; Moritz, 2002; Smith *et al.*, 2005). One such surrogate of diversity is environmental variability, and thus by conserving species across the suite of environmental conditions that they occupy one stands a better chance of conserving intra-specific diversity for many species.

Large-scale deforestation in some regions of the world (e.g. the northern Andes, Atlantic forests of Brazil) may have already greatly limited our opportunities to conserve intra-specific diversity. In the Atlantic forests more than two-thirds of bird species are considered rare (Goerck, 1997) and the region contains the greatest proportion of threatened species in the Neotropics (Stotz *et al.*, 1996). Furthermore, recent studies using palaeoclimatic models and molecular-based phylogenies have identified areas within the Atlantic forests that harbour greater genetic diversity and high levels of endemism (Cabanne *et al.*, 2008; Carnaval *et al.*, 2009; see also da Silva *et al.*, 2004; Carnaval & Moritz, 2008). Such areas are hypothesized to contain higher levels of genetic diversity as they experienced greater climatic stability during the late Quaternary (Carnaval & Moritz, 2008).

Here we assess the impacts of extensive deforestation on both reduction in area potentially occupied and environmental niche space (range of environmental conditions) for a suite of birds in the Atlantic forests of Brazil as a means to evaluate the potential opportunities remaining (or lost) for conservation of diversity in this region. We also compare how environmental conditions in the Atlantic forest biome have changed as a function of deforestation and how they are expected to change under future climate scenarios. Previous examination of forest loss in Atlantic forest birds has focused primarily on changes in range size and the identification of current hotspots of diversity for threatened species (e.g. Harris & Pimm, 2004, 2008; Harris *et al.*, 2005). The novelty of this study is the examination of the consequences of both deforestation and future climate change for the environmental niches of birds.

MATERIALS AND METHODS

Study species

Birds of the family Cotingidae and Pipridae (order Passeriformes: class Aves) are restricted to the New World tropics. Cotingids vary markedly in size, from the tiny kinglet calyptura (*Calyptura cristata*) (8 cm body length) to umbrellabirds (up to 49 cm body length), some of the largest passerine birds (Ridgley & Tudor, 1994), while piprids are generally small (9–15.5 cm body length). Both groups are primarily arboreal frugivores, although many supplement their diet with invertebrates (Sick, 1993). We included 12 cotingid and nine piprid species that occur in the Atlantic forests of eastern Brazil (here we follow nomenclature as presented in Ridgley & Tudor, 1994, except as noted). We excluded two cotingids [kinglet calyptura (*C. cristata*) and grey-winged cotinga (*Tijuca condita*)] because of the paucity of museum specimens for these species, and with the exception of the two *Schiffornis* species, we only included piprids that are considered 'true' manakins (see Prum, 1994; Ridgley & Tudor, 1994). It should be noted, however, that the evolutionary history of these species is complicated and under revision. Current molecular work suggests that a number of the species included here as Cotingidae or Pipridae may be separated into different groups (Tello *et al.*, 2009). Of these 21 species, nine are considered globally threatened (IUCN, 2009).

Historical range models

Data sources

The historical range models produced here required: (1) verified locational data on bird species, (2) environmental maps depicting pre-disturbance conditions, and (3) maps delimiting species range extents to provide boundaries on modelled distributions. Locational data for birds came from museums and private collections in North America and Brazil, and for the nine globally threatened species from BirdLife International. Locational data were recorded directly from the specimen tag, or generated later using locality descriptions from ornithological gazetteers (Paynter & Traylor, 1991) and supplements (Vanzolini, 1992). Individual locations were then double-checked by the authors (principally J.M.G.) and discarded when accuracy was in doubt (e.g. species occurring outside of a known elevational range). Overall, 722 independent natural history records ('independent' being here defined as records that are at least 1 km distant from other records for a given species) ranging from 4 (*Tijuca atra*) to 158 (*Chiroxiphia caudata*) were recorded for the 21 species in eastern Brazil. These localities are distributed throughout the coastal states within the Atlantic forest region of Brazil (Fig. 1).

We used climatic variables derived from the WORLDCLIM Version 1.3 database (http://www.worldclim.org; Hijmans *et al.*, 2005) to model the potential distributions of birds. WORLDCLIM is a set of global climate layers (grids) on a
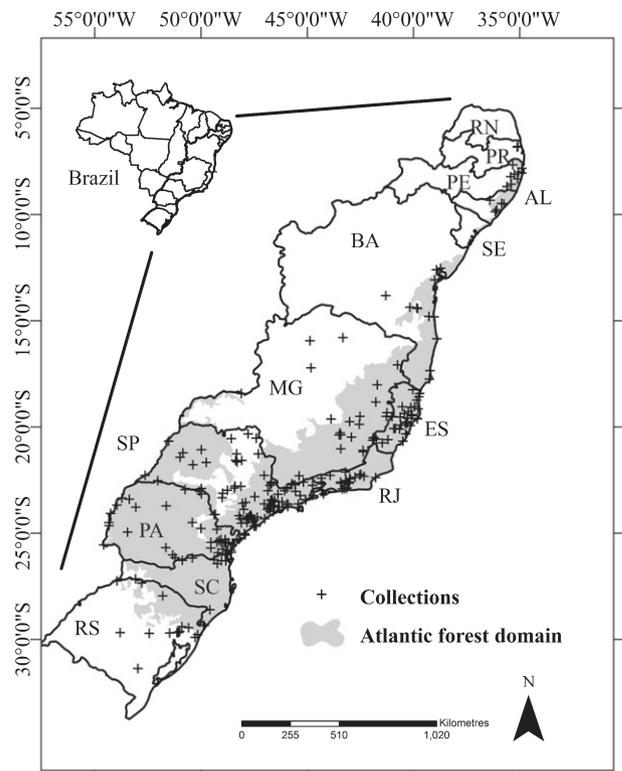
Figure 1 Distribution of voucher localities in eastern Brazil for bird species modelled in this study. In the main map, the 13 states where voucher specimens were included are: AL, Alagoas; BA, Bahia; ES, Espírito Santo; MG, Minas Gerais; PA, Paraná; PE, Pernambuco; PR, Paraíba; RJ, Rio de Janeiro; RN, Rio Grande do Norte; RS, Rio Grande do Sul; SC, Santa Catarina; SE, Sergipe; SP, São Paulo.

30-arcsec resolution grid (*c.* 900 m × 900 m). The climatic data layers were generated by interpolating average monthly climate data over a period of *c.* 30 years from weather stations around the world. We used nine variables: mean annual temperature, mean diurnal range in temperature [mean of monthly (max temp − min temp)], temperature seasonality (standard deviation × 100), temperature of coldest quarter, temperature of warmest quarter, mean annual precipitation, precipitation seasonality (coefficient of variation), precipitation of wettest quarter, and precipitation of driest quarter. These climatic variables are commonly used in ecological niche modelling and reflect annual trends (e.g. mean annual temperature), seasonality (e.g. annual range in precipitation) and extreme environmental factors (e.g. temperature of the coldest quarter) (Hijmans *et al.*, 2005).

We used three future climate scenarios for 2050 that were derived from IPCC climate surfaces – CSIRO-MK3.0; CCCMA-CGCM3.1-T63 and GFDL-CM2 (Ramirez & Jarvis, 2008) (http://gisweb.ciat.cgiar.org/GCMPage/). We use these climate models because they represent a range of the available climate models and there is no agreement in the literature as to which models are most appropriate for predicting future

species distributions (Pierce *et al.*, 2009). Selection of several models allows us to examine the general robustness of our results. These climate surfaces were downscaled using a spline interpolation algorithm of the anomalies and the current distribution of climates from the WORLDCLIM database (Ramirez & Jarvis, 2008). The same climate variables as described above were used for 2050 climate surfaces.

We used the Mapa de Vegetação do Brasil (IBGE, 1988), which was digitized at the US Geological Survey's (USGS) EROS Data Center, Sioux Falls, SD, to define the historical range of Atlantic forests in Brazil (http://na.unep.net/). Within Brazil, our reclassification indicated that the Atlantic forests originally covered an area of about 862,900 km^2; the estimated original area of Atlantic forests is 1,233,875 km^2 when forested areas that cross into Paraguay and Argentina are included (http://www.biodiversityhotspots.org/xp/hotspots/atlantic_forest/Pages/default.aspx). Our classification of the Atlantic forest ecosystem is conservative compared with another recent estimate (Ribeiro *et al.*, 2009). However, Ribeiro *et al.* (2009) included seasonal deciduous forests; these additions lead to estimations that original forest in Brazil occupied 1,395,849 km^2.

Species distribution models

We modelled species distributions using MAXENT (Phillips *et al.*, 2006). We selected MAXENT because of its consistently high performance in a study that tested 17 different model algorithms in six regions (Elith *et al.*, 2006). We also used two other estimates of a species' distribution: (1) genetic algorithm for rule-set prediction (GARP) to generate species distribution models, and (2) extent of occurrence (EOO) maps (see below). GARP has been used widely for modelling data from natural history collections (e.g. Peterson, 2001). As qualitative results regarding environmental niches were very similar between the two modelling methods we give methods and results from MAXENT and EOO only for ease of presentation. As some models were derived with fewer than 10 localities, we highlight these species and emphasize results from EOO data.

MAXENT estimates a species' distribution by determining the distribution of maximum entropy (i.e. that is closest to uniform) under the constraint that the expected value of each climate predictor under this estimated distribution matches its empirical average (Phillips *et al.*, 2004). We set the 'regularization multiplier' parameter to 1 (default) to avoid over-fitting the data; the number of maximum iterations and convergence threshold were set at default values of 500 and 0.00001, respectively. We used 25% of museum localities for each species as the random test percentage. The area under the receiver operating characteristic curve (area under the curve, AUC) was selected to evaluate the predictions using the test data. As no true absence data are available, MAXENT uses fractional predicted area (the fraction of the total study area predicted present) as specificity rather than true commission (fraction of absences predicted present) (Phillips *et al.*, 2006). AUC has been used extensively in the species distribution modelling literature; AUC measures the ability of a model to discriminate between sites where a species is present and where it is absent (Fielding & Bell, 1997). AUC values range from 0 to 1, where a score of 1 indicates perfect discrimination and a score of 0.5 implies discrimination that is no better than random. A map of the range extent of the species (EOO; digitized from Ridgley & Tudor, 1994) was developed and then used to limit the predicted historical area of occupancy for the species (hereafter referred to as MAXENT-historical distribution). This final step basically imposes historical barriers onto the model. Such barriers reflect both physical (e.g. mountain ranges, major rivers) and/or biotic (e.g. occurrence of sister species) limitations to species ranges. We also used EOO as an alternative prediction of the historical distribution (EOO-historical distribution). In this case, the EOO was corrected so that it included only vegetation considered within the Atlantic forest biome in order to match known habitats and environments of the target species.

Current ranges

Predicted historical distribution maps for each species were combined with a 1991 digital coverage depicting forest remnants such that only historical areas predicted to be occupied that still contain forest are included in the current distribution. The forest remnant coverage used to derive the current distribution of birds includes six states within the Atlantic forest region of Brazil; these six states include > 70% of the forest within the region. All measures of range and environmental niche reduction are based on these six states only. The forest cover map was derived from multi-temporal TM/Landsat-5 satellite imagery provided by the SOS Mata Atlântica and National Institute for Space Research (INPE) in Brazil. The smallest remnant identified in this map is *c.* 100 ha (*c.* 1 km × 1 km). Analysis of the remnant coverage suggests that only 7.5% of the original forest cover remains (Fig. 2). This figure closely approximates other estimates of Atlantic forest remaining [8%, SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais (INPE), 1993; 10%, Harris & Pimm, 2004; 7%, as reported by SOS Mata Atlântica, INPE, 2008]. Our estimates, which were based on satellite images taken between 1985 and 1991, do not reflect subsequent land-use changes and probably also include secondary growth and disturbed forest (Tabanez & Viana, 2000), which do provide suitable habitat for some of our study species. Ribeiro *et al.* (2009), however, estimated that *c.* 12% of forest remains in the Atlantic forest. This new estimate is higher than other estimates probably because it includes early successional forests and fragments < 100 ha in size.

Measures of the impact of deforestation

The impact of forest loss on bird species distributions was measured by: (1) total and percentage reduction in area occupied, and (2) shifts in environmental conditions occupied by birds between pre- and post-disturbance distribution maps. To quantify reductions in the total and percentage area of
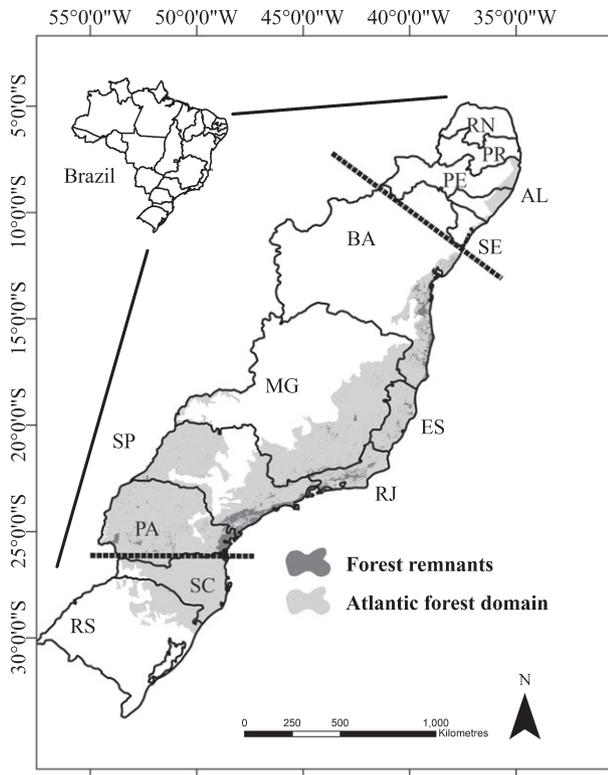
Figure 2 Estimated original distribution of Brazilian Atlantic forests (light- and dark-shaded areas combined) and forests remaining (dark-shaded) based on analysis of 1985–91 satellite images (see Materials and Methods for a description of how forest cover was generated). Dashed lines indicate the northern and southern boundary for analysis of forest loss within the Atlantic forests region (i.e. states of Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro and São Paulo). Here we only include those states located along the coast; states with some Atlantic forest not included in these analyses were Mato Grosso do Sul, Ceará and Piauí. Within these boundaries, an estimated 92.5% of original forest has been lost. State boundaries are indicated on the map (see Fig. 1).

Atlantic forest biome, as well as that predicted to be occupied by a given bird species, forest and species distribution maps were projected into equal area grids with a cell size of 1 km^2 resolution. The total forest area in the region or area occupied by a given bird species was then tabulated and compared for historical (pre-) and current (post-) deforestation conditions to determine the potential proportion of area that was lost due to deforestation in the region. When necessary, the proportion of area lost was corrected to include only those states for which deforestation data existed (i.e. parts of species ranges that extend beyond the remnant forest map were omitted in determining the proportion of area remaining).

To determine changes in the environmental niche occupied by a given species or within the Atlantic forest biome pre- and post-deforestation, we used environmental niche factor analysis (ENFA) (Hirzel *et al.*, 2002). ENFA is a multivariate approach that compares the multidimensional space of

ecological variables between two data sets. It has principally been used to compare the environment of known localities of a target species with that observed in the study or reference area. The first factor extracted maximizes the marginality of the focal species. Marginality is defined as the ecological distance between the species optimum and the mean habitat within the reference area (see Figures 1 and 2 in Hirzel *et al.*, 2002). The remaining factors measure the specialization of the target species, which reflects the variance of the environmental conditions of the species relative to the reference area. In this study the reference area was defined as the historical distribution (Maxent-historical, EOO-historical) for each species, or the original extent of the Atlantic forest biome (see Fig. 1). We then used the projected current distribution (i.e. the historical distribution corrected to include only areas that still remain forested) as the locality data. To do this, we extracted lat-, long-coordinates for every grid cell that is predicted to be suitable under current conditions for comparison with original Atlantic forest. We used the 'enfa' function from the package 'adehabitat' (Calenge, 2009) to run the analysis in R (R Development Core Team, 2007). Prior to running the ENFA, the raster maps that contained values of nine environmental variables for each grid cell in the historical distribution or the original Atlantic forest were converted to ascii format and combined into a multi-layer map of class *kasc* in R. As ENFA requires that environmental variables are transformed (e.g. column-centred and standardized) we transformed all climate variables such that each had a mean of 0 and a variance of 1. The resultant ENFA then can be interpreted similarly to a principal components analysis (PCA) with eigenvalues and loadings for each variable along the axis of marginality (first axis) and successive orthogonal axes that represent specialization (see Hirzel *et al.*, 2002; Calenge, 2009). In addition, ENFA provides a marginality score. Here we report only the results of the marginality axis as our question focused on how mean environments of species distributions have shifted due to deforestation.

We tested the significance of changes in environmental niche due to deforestation using a randomization procedure in R ('randtest.enfa'; Calenge, 2009). Randtest.enfa simulates a random distribution of the species predicted occurrences in the historical distribution (or original forest); we used 999 repetitions in the simulation. At each step, the test randomly allocates the number of occurrences that can be found in the current predicted distribution (or remnant forest) in the pixels of the reference area (i.e. historical distribution or original forest cover). The first eigenvalue of the ENFA performed on the randomized dataset is recomputed during each simulation and the observed value is compared with the distribution of the simulations to test the significance of the ENFA analysis.

Estimating the impact of future climate change

To estimate the relative impact of changing climates on environmental conditions in the Atlantic forest biome, we

used analysis of similarity (ANOSIM) and PCA to compare how environments have changed in response to deforestation and how they might change in the future based on 2050 climate models. To do this, we selected a set of random locations within the extent of the original Atlantic forest ecosystem and within the remnant forests. These two sets of random locations were independent in the sense that we excluded remnant forest locations from the original Atlantic forest prior to selecting random locations. As forest remnants are generally small patches, this did not affect the geographic extent of selection of random sites within the original Atlantic forests. For PCA, 8000 and 1000 locations were selected from original and remnant forest, respectively; however, for ANOSIM only 2000 and 500 locations from the original set of random locations were selected because of limitations in running Monte Carlo simulations. At each of these random locations, values for each of the nine climate variables were extracted to produce a site by climate matrix. The matrix included present-day climate values for original and remnant forest locations and future climate values for remnant forests. For these analyses we did not include future climates within the original extent of forest as such conditions are not relevant due to past deforestation. As for ENFA, climate variables within the matrix were transformed such that each variable had a mean of 0 and variance of 1. We used ANOSIM (see the description in Clarke & Warwick, 2001), a permutation-based analysis, to test the hypothesis that the three groups (original forest–present climate, remnants–present climate, remnants–future climate) differ in environmental conditions. To do this, ANOSIM compares the level of similarity among a set of related samples (e.g. original forest–present climate versus remnants–present climate) to the level of similarity across all samples to determine if forests differed in environmental conditions more than expected by chance. The significance of the ANOSIM test statistic is determined by comparison with values obtained by a Monte Carlo randomization procedure; here we used 999 repetitions in our Monte Carlo procedure.

We visualized the differences in environments among these three groups using PCA. PCA reduces the set of nine climate variables into a set of independent orthogonal axes, and random locations described above are depicted along the axes with respect to their similarity in environmental conditions. PCA ordination allowed us to examine how the various forest environments (original forest–present climate, remnant–present climate, remnant–future climate) overlapped in environmental space. We calculated the mean scores for the three forest environments along the main principal components axes to provide an idea of how deforestation and climate change affect forest environments. Differences among the three groups in the environmental ordination were examined using a one-way analysis of variance followed by *post hoc* comparisons. We used the program PRIMER (Clarke & Gorley, 2006) for ANOSIM and PCA.

RESULTS

Changes in Atlantic forest cover

Environments within the original Atlantic forest region were quite varied, with mean annual temperature ranging from *c.* 8.8 to 25.8 °C and mean annual precipitation ranging from *c.* 400 to 3000 mm. We found that environments present in forest remnants today are significantly different from those found in original or 'historical' forest cover (marginality = 3.13, $P < 0.001$; Table 1). Remnants are characterized by a lower diurnal range in temperatures, and greater and less seasonal annual precipitation, primarily due to a wetter dry season (see Fig. S1 in Supporting Information). These large-scale environmental changes may be a result of the nearly complete loss of plateau and interior forests within the Atlantic forest region and reflect both the heterogeneous nature of the Atlantic forest region and the non-random pattern of forest loss.

Historical avian distribution maps

Historical distribution models estimate that birds occupied areas from *c.* 50,000 to 1,100,000 km² (Table 2). MAXENT models performed well with a mean (± SD) AUC value of 0.931 ± 0.014 (AUC values of individual models ranged from 0.801 to 0.992); all MAXENT models were significant ($P < 0.001$). The percentage of suitable habitat within the

Table 1 Results of environmental niche factor analysis (ENFA) that compare environmental conditions of Brazilian Atlantic forest remnants (≥ 100 ha) with 'historical' vegetation (i.e. prior to anthropogenic loss of forest cover) based on present climate. Marginality value, eigenvalues and variance explained for the marginality axis (of a total of nine) are shown in the upper portion of the table and coefficient values for each of the nine climatic variables on these axes are shown in the lower portion of the table. ENFA was highly significant ($P < 0.001$) when compared against random simulation (see Materials and Methods). Positive values of the marginality factor indicate that the present-day environmental conditions are higher in value than those of the potential or 'historical' conditions.

	Historical versus forest remnants
Marginality	3.13
Eigenvalue (% variance)	2.2 (27.2)
Annual mean temperature	−0.096
Temperature diurnal range	−0.654
Temperature seasonality	0.038
Mean temperature warmest quarter	−0.055
Mean temperature coldest quarter	−0.060
Annual precipitation	0.529
Precipitation seasonality	−0.307
Precipitation wettest quarter	0.188
Precipitation driest quarter	0.382

Species	Range extent	Potential distribution	Current distribution	Remaining (%)
Cotingidae				
Carpornis cucullata (25)	348,832	282,208	29,799	22.5
Carpornis melanocephala (24)	341,409	263,476	37,378	21.5
*Cotinga maculata** (6)	237,671	214,267	18,078	9.0
Iodopleura pipra (12)	188,170	167,607	24,033	20.5
Laniisoma elegans (20)	436,533	271,338	20,590	10.1
Lipaugus lanioides (28)	627,118	437,384	30,689	10.0
Lipaugus vociferans (16)	244,887	221,914	13,290	12.5
Phibalura flavirostris (29)	1,150,818	822,921	38,454	7.4
Procnias nudicollis (53)	1,534,838	605,177	34,946	9.8
Pyroderus scutatus (40)	1,809,550	951,178	41,747	6.9
*Tijuca atra** (4)	50,348	50,348	10,595	21.8
*Xipholena atropurpura** (9)	250,038	156,002	17,329	14.3
Pipridae				
Chiroxiphia caudata (158)	1,494,005	1,103,331	40,640	6.7
Chiroxiphia pareola (13)	195,615	179,880	14,745	16.2
Ilicura miltaris (45)	865,421	532,559	33,316	8.5
Manacus manacus (101)	1,075,000	892,104	43,180	6.8
*Machaeropterus regulus** (9)	157,780	151,975	18,199	13.2
Pipra pipra (12)	105,940	80,909	8444	12.6
Pipra rubrocapilla (24)	169,973	127,033	7307	10.4
Schiffornis turdinus (16)	203,917	133,642	7575	8.8
Schiffornis virescens (78)	1,275,794	871,178	37,655	7.2

Table 2 Area estimates (km^2) of range extent, potential distribution and current distribution (i.e. the portion of potential distribution that remains forested) for selected bird species within Cotingidae and Pipridae in Brazilian Atlantic forests. Potential distributions were based on Maxent models except where noted (see Materials and Methods). The estimated percentage range remaining {100 − [(current distribution × 100)/(potential distribution)]} is also provided. When necessary, for this latter estimate the potential distribution was corrected to include only those areas for which data on current forest cover were available. The number of localities available for modelling is provided in parentheses following each species name.

*For these species, results are reported using range extents rather than Maxent models because the number of localities was < 10. The range extent is the total area within the range extent, potential distribution only includes parts of the range extent that are considered within the Atlantic forest ecosystem, and current distribution is given by the sum of forest remnants still remaining within the range. As for species modelled by Maxent, the percentage remaining, if necessary, was corrected to include only those areas in which data on current forest cover are available.

range extent (EOO) using Maxent models was predicted to range from 39% to 92% (72.2 ± 3.3% SE) (i.e. as given by the potential distribution/range extent in Table 2). The conservation status of birds did not appear to be associated with estimates of historical distribution. Globally threatened species do not have smaller historical ranges than non-threatened taxa (Mann–Whitney $U = 49$, $P > 0.75$). Moreover, there were no differences in the percentage of suitable habitat within the range between globally threatened and other taxa ($U = 31$, $P > 0.80$).

Impact of deforestation on historical ranges

Overlaying the forest remnant map revealed that birds are estimated to have from 6.7% to 22.5% of their original ranges remaining in forest cover (Table 2). Reductions were marginally related to conservation status as reductions of globally threatened taxa (mean = 84.8%) were less than those of non-threatened taxa (mean = 90.0%; Mann–Whitney $U = 27$, $P = 0.055$ for percentage reduction). The size of historical ranges, however, was positively related to the percentage reduction of species range; larger ranges experienced relatively greater reductions (Spearman's $\rho = 0.692$, $n = 21$, $P < 0.001$).

Forest loss in the north-east and south-west portions of the Atlantic forests has been particularly high (Fig. 2). Consequently, birds whose ranges extend into these areas [e.g. red-ruffed fruitcrow (*Pyroderus scutatus*), swallow-tailed cotinga (*Phibalura flavirostris*), blue manakin (*Chiroxiphia caudata*)] have disproportionately less of their original range remaining, while those whose ranges are centred on the Serra do Mar area along the south-east coast have more habitat remaining [e.g. hooded berryeater (*Carpornis cucullata*), black-and-gold cotinga (*Tijuca atra*)].

We found significant shifts in environmental conditions between historical and current distributions for all 21 species using either estimates based on range extents (EOO) or Maxent models (Table 3). As with the Atlantic forest biome, the available environmental niche of most birds has shifted to greater annual rainfall and less seasonal rainfall with lower diurnal and seasonal variation in temperature (Table 4).

Impacts of future climate change

Atlantic forest organisms can expect to experience significant changes in future climates (Table 5, Fig. 3). Assuming no

Table 3 Results of environmental niche factor analysis that compare environmental conditions of potential or 'historical' distribution for selected bird species within Cotingidae and Pipridae (i.e. prior to anthropogenic loss of forest cover) with 'current' distribution (i.e. after correction for forest remaining) in Brazilian Atlantic forests. Marginality values (M) and results of randomization test (P-value) are provided for distributions based on range extent (extent of occurrence, EOO) or based on Maxent models.

Species	EOO		Maxent	
	M	P-value	M	P-value
Cotingidae				
Carpornis cucullata	2.98	0.001	2.10	0.001
Carpornis melanocephala	2.09	0.001	1.75	0.001
Iodopleura pipra	3.02	0.001	2.80	0.001
Laniisoma elegans	6.88	0.001	5.23	0.001
Lipaugus lanioides	6.81	0.001	7.40	0.001
Lipaugus vociferans	3.03	0.001	3.10	0.001
Philabura flavirostris	4.28	0.001	3.95	0.001
Procnias nudicollis	2.71	0.001	3.66	0.001
Pyroderus scutatus	3.35	0.001	3.94	0.001
Tijuca atra	1.20	0.001	1.13	0.001
Xipholena atropurpura	1.29	0.001	2.02	0.001
Pipridae				
Chiroxiphia caudata	3.31	0.001	4.47	0.001
Chiroxiphia pareola	1.07	0.001	1.22	0.001
Ilicura militaris	5.13	0.001	5.33	0.001
Manacus manacus	3.09	0.001	4.06	0.001
Machaeropterus regulus	1.68	0.001	2.96	0.001
Pipra pipra	1.56	0.001	2.98	0.001
Pipra rubrocapilla	1.19	0.001	0.89	0.001
Schiffornis turdinus	4.71	0.001	4.83	0.001
Schiffornis virescens	5.18	0.001	4.98	0.001

Table 4 Climatic variables that show the highest coefficient scores along the marginality axis in environmental niche factor analysis (ENFA) that compares environmental conditions of potential or 'historical' distribution for selected bird species within Cotingidae and Pipridae (i.e. prior to anthropogenic loss of forest cover) with 'current' distribution (i.e. after correction for forest remaining) in Brazilian Atlantic forests. Only the three variables (of nine) with the highest coefficient scores are shown. Positive values indicate that climatic values for current conditions are greater than historical conditions. Results are presented for ENFA conducted using species distributions based on range extent (extent of occurrence, EOO) or Maxent models.

Species	EOO	Maxent
Cotingidae		
Carpornis cucullata	PA(+), PDQ(+), TDR(−)	PA(+), PDQ(+), TDR(−)
Carpornis melanocephala	PA(+), PDQ(+), PWQ(+)	PA(+), PDQ(+), PWQ(+)
Iodopleura pipra	PDQ(+), PA(+), TS(+)	PDQ(+), PA(+), TS(+)
Laniisoma elegans	PA(+), TDR(−), PDQ(+)	TDR(−), PA(+), PDQ(+)
Lipaugus lanioides	PDQ(+), TDR(−), PA(+)	PDQ(+),TDR(−), PA(+)
Lipaugus vociferans	PDQ(+), TDR(−), TS(−)	PDQ(+), TS(−), TDR(−)
Philabura flavirostris	TDR(−), PA(+), PWQ(+)	TDR(−), PA(+), PWQ(+)
Procnias nudicollis	TDR(−), PA(+), PWQ(+)	PA(+), TDR(−), PWQ(+)
Pyroderus scutatus	TDR(−), PA(+), PDQ(+)	TDR(−), PA(+), PWQ(+)
Tijuca atra	PA(+), PDQ(+), PWQ(+)	TA(+), TWQ(+), TDR(+)
Xipholena atropurpura	PA(+), PDQ(+), TDR(−)	PDQ(+), TDR(−), TS(−),
Pipridae		
Chiroxiphia caudatat	TDR(−), PA(+), PDQ(+)	TDR(−), PA(+), PDQ(+)
Chiroxiphia pareola	PA(+), PDQ(+), TWQ(−)	PDQ(+), PA(+), TDR(−)
Ilicura militaris	TDR(−), PA(+), PWQ(+)	TDR(−), PA(+), PWQ(+)
Manacus manacus	TDR(−), PA(+), PDQ(+)	PWQ(−), TWQ(+), AT(+)
Machaeropterus regulus	PA(+), PDQ(+), TDR(−)	PDQ(+), TDR(−), PS(−)
Pipra pipra	PA(+), TWQ(−), PDQ(+)	PDQ(+), PA(+), TDR(−)
Pipra rubrocapilla	PA(+), PDQ(+), TDR(−)	PDQ(+), PA(+), TDR(−)
Schiffornis turdinus	PDQ(+), TDR(−), PS(−)	PDQ(+), PA(+), TDR(−)
Schiffornis virescens	TDR(−), PA(+), PDQ(+)	TDR(−), PA(+), PWQ(+)

AT, mean annual temperature; TDR, temperature diurnal range; TS, temperature seasonality; TWQ, mean temperature warmest quarter; PA, annual precipitation; PS, precipitation seasonality; PDQ, precipitation in driest quarter; PWQ, precipitation in wettest quarter.

additional change in forest cover over the next several decades, environmental conditions in forest remnants in 2050 are predicted to be warmer and to experience less seasonal variation in temperatures. Future climates in forest remnants when compared with original Atlantic forests will also be less seasonal with respect to precipitation, largely due to increased

	PC 1	PC 2	PC 3
Eigenvalue (% variance)	3.86 (42.9)	2.49 (27.6)	1.47 (16.3)
Variable			
Mean annual temperature	−0.482	0.022	−0.084
Mean diurnal range temperature	0.195	−0.308	0.470
SD monthly temperature	0.357	0.174	0.260
Mean temperature warmest quarter	−0.434	0.107	−0.047
Mean temperature coldest quarter	−0.494	−0.011	−0.163
Annual precipitation	0.317	0.215	−0.529
Precipitation seasonality (CV)	0.018	−0.616	−0.152
Precipitation wettest quarter	0.248	−0.258	−0.608
Precipitation driest quarter	0.092	0.609	−0.053
Means*			
Original Atlantic forests	0.023[a]	−0.234[a]	0.235[a]
Forest remnants–present	0.035[b]	0.884[b]	−0.763[b]
Forest remnants–future	−0.050[c]	0.718[c]	−0.842[b]

Table 5 Results of principal components (PC) analysis examining Brazilian Atlantic forest environments under present and future climate conditions. The ordination depicts environments found at random locations within the original Atlantic forest ecosystem and forest remnants under present climate and forest remnants in future climates. Here we depict future climates based on CSIRO-MK3.0 only, as all future climate scenarios provide qualitatively similar results. Only axes with eigenvalues > 1 are shown in the table. Eigenvalues and percentage variance explained are provided in the upper portion of the table, while factor loadings for each environmental variable on each of the three axes with eigenvalues > 1 are shown in the lower portion of the table. Means ± SD are given for the three groups depicted in Fig. 3 are provided in the last three rows.

CV, coefficient of variation; SD, standard deviation.

*Significant differences between mean scores of the three groups (original Atlantic forests, forest remnants–present, forest remnants–past) along each of the three principal component axes are indicated by different superscript letters; analysis was based on *post hoc* comparisons following MANOVA.

rainfall during the driest quarter; this latter result reflects the difference already observable in today's forest remnants. However, the greatest changes in environmental conditions are seen as a result of deforestation (ANOSIM analysis: $R = 0.225$ and 0.245, $P < 0.001$ for comparison between original forest–present day remnants, original forest–2050 remnants, respectively), while environmental conditions in remnants under current climates and 2050 climates are more similar, but still significantly different ($R = 0.035$, $P < 0.001$; global $R = 0.225$, $P < 0.001$). Nonetheless, environmental conditions in 2050 forest remnants occupy novel environmental space, with locations being warmer than any time in the recent past (see Fig. 3). All three future climate scenarios largely agreed on these predicted outcomes so only results from the CSIRO-MK3.0 climate scenario are shown.

DISCUSSION

The Atlantic forests are considered one of the world's biodiversity hotspots and harbour high numbers of endemic species (Myers *et al.*, 2000; Tabarelli *et al.*, 2005). Deforestation in the region has caused significant declines in suitable habitat and shifts in environmental niche space for nearly all species of birds examined in this study. Declines in suitable habitat for globally threatened taxa were slightly less, on average, than those for other taxa (84.8% vs. 90%). This result is consistent with the findings of Harris & Pimm (2004), who found that the impacts of deforestation were general and that both forest obligate birds and those that tolerated secondary forests were affected by changes in forest cover. In terms of shifts in available environmental niche space, Atlantic forest birds today experience generally wetter and less seasonal forest

environments than they did prior to recent patterns of deforestation. These results suggest that selective regimes may have shifted with anthropogenic change due to habitat destruction, and thus spatial patterns of intra-specific variation in morphology, behaviour and genes have probably been altered. Indeed, a reduction in temperature and rainfall seasonality, as well as shifts along precipitation and temperature gradients experienced by birds, may have resulted in a general decrease in genetic diversity and shifts in allelic frequencies, especially if cryptic variation exists in response to different environmental conditions. The potential impacts on genetic diversity caused by deforestation and changes in environmental conditions may be great when one also considers the past evolutionary history of the region.

In Atlantic forests today, hotspots of threatened bird species occur primarily in the lowland forests of Rio de Janeiro (Harris *et al.*, 2005), but many locations, such as those in central and north-east Atlantic forests, harbour significant numbers of species at risk of extinction (Important Bird Areas; Bencke *et al.*, 2006). Birdlife/SAVE Brazil has identified 16 of the 163 Important Bird Areas as priority areas for immediate conservation action (http://www.savebrasil.org.br/ingles/3projetos_areas.asp); these high-priority areas include both coastal and interior forests from northern-most sites in Ceara to southern-most sites in Rio Grande do Sul. Regions of high risk correspond to predicted forest refuges within the Atlantic forests (Carnaval *et al.*, 2009). The largest of these is in the central portion of the Atlantic forests (Bahia refugium), while smaller refugia were identified in the north-east (Pernambuco refugium) and south-east (São Paulo refugium). Studies on different taxa have found that the larger central forest refuge harbours the greatest genetic diversity, while the north-east
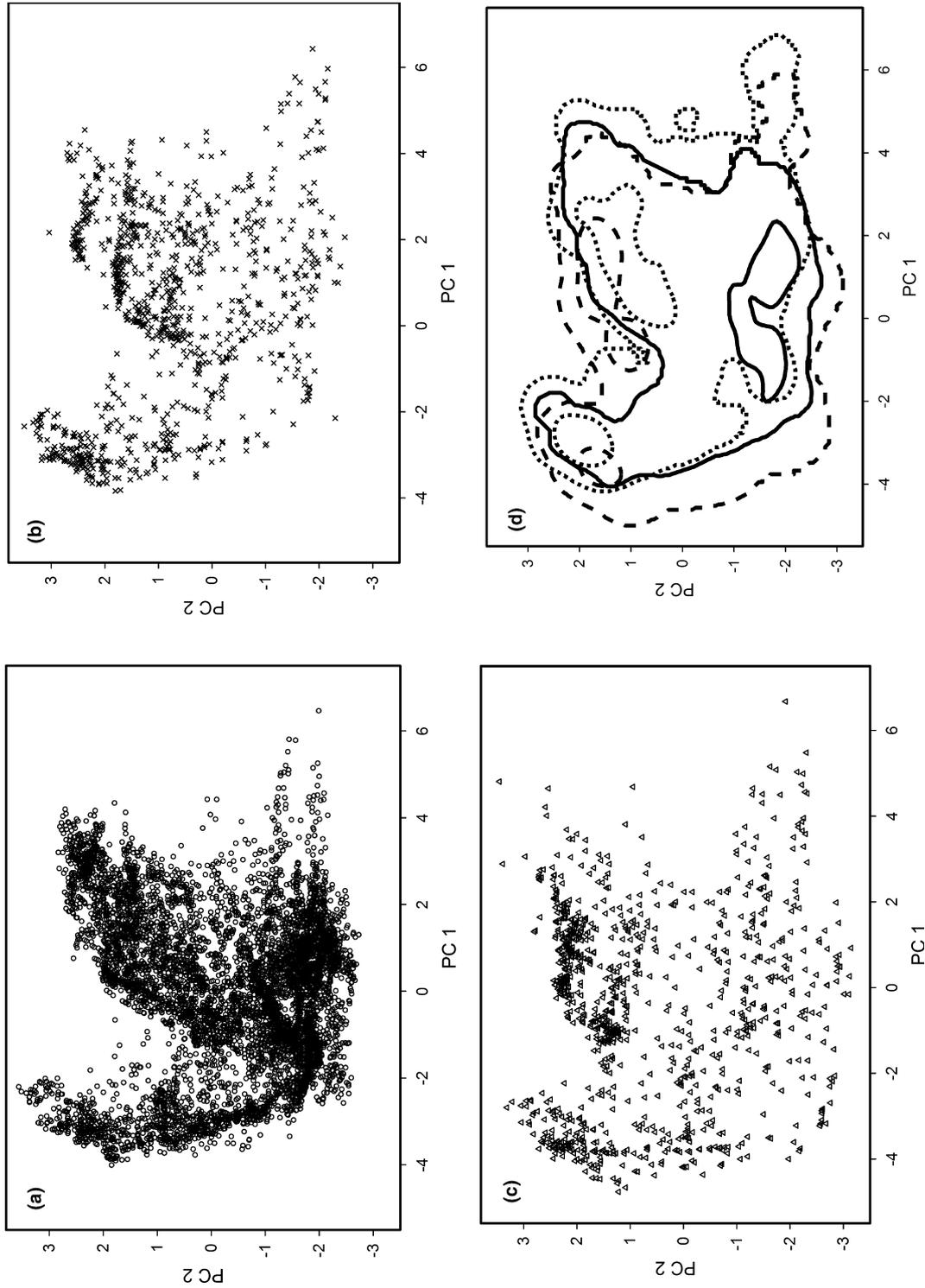
Figure 3 Results from principal components analysis (PCA) that projected random locations within Brazilian Atlantic forests into environmental space based on nine climate variables. Climate variables were transformed to mean of 0 and variance of 1 prior to ordination. The results are divided for clarity: (a) represents locations within original Atlantic forests under present climate (excludes any forest remnant location) and are depicted as circles (○), (b) represents forest remnant locations under present climate depicted as cross-hairs (×), (c) represents forest remnant locations under predicted 2050 climate based on CSIRO-MK3.0 scenario depicted as open triangles (△), (d) shows 50% and 95% contour intervals encompassing points for original forests (solid line), present-day remnants (dotted line) and 2050 forest remnants (dashed line). Factor loadings and mean scores for these three groups for first three principal components are provided in Table 5.

refuge is generally the most distinct, indicating a longer period of differentiation among taxa (Cabanne *et al.*, 2008; Carnaval *et al.*, 2009). We found that the central and north-east Atlantic forest regions have experienced relatively greater loss of forest than the south-east region (da Silva & Tabarelli, 2000; Ribeiro *et al.*, 2009; Fig. 2). As these regions possess genetically diverse and distinct taxa, Carnaval & Moritz (2008) suggest that not only might considerable unique diversity be lost, but the signature of historical processes that led to current patterns of biological diversity could also disappear.

We know of no detailed genetic analyses that document how changes in environmental conditions influence birds in the Atlantic forest. Nonetheless, there is increasing evidence that genetic variation in lineages or clades is often related to broad climatic parameters such as those measured in this study. Graham *et al.* (2004) showed that sister taxa of dendrobatid frogs differed in the environmental space used, and suggested that divergent selection was likely to be an important driver of speciation. In a related study, Thomassen *et al.* (2009) showed that intra-specific morphological variation in wedge-billed woodcreepers in the Ecuadorian Amazon was strongly correlated with environmental conditions. These studies have not addressed how deforestation and associated changes in environmental conditions will influence genetic and other types of diversity. We hope that the methodology we present here will stimulate new approaches to conservation that integrate geographic/environmental analyses, such as distributional modelling and land-cover change, with studies of genetic, morphological and behavioural variation across species ranges.

The conservation of inter- and intra-specific diversity in Atlantic forest organisms is a great challenge given the large reductions in forest area. Further complicating this picture are the predictions of how Atlantic forest environments will change in the future. Future forests are predicted to become warmer, and experience less seasonal variation in temperatures. Like present-day conditions in remnants, future climates in remnant forests are also likely to have lower annual variation in precipitation due largely to greater rainfall during the dry season. However, organisms living in forest remnants in 2050 will experience conditions that are warmer than any time in the recent past. Our findings of warmer environments that represent novel environments match results expected generally for tropical lowland forests (Colwell *et al.*, 2008); indeed this study reports that tropical lowland environments will be hotter than anything experienced in the last 2 Myr. Unless organisms can adapt to these novel environments, Colwell *et al.* (2008) predict that lowland habitats will undergo biotic attrition (i.e. suffer reduced species diversity).

Due to limited resources to adequately survey the genetic diversity and structure of all but a few species, efforts should be directed to conserve surrogates of intra-specific diversity, such as conserving sites along the environmental gradients that species occupy (Margules & Pressey, 2000; Smith *et al.*, 2005). In Atlantic forests, the option to conserve entire environmental gradients has probably been lost in some cases, because what represented common climatic environments historically are at best rare today. Nevertheless, an environmental analysis of forest remnants in an area may help target conservation efforts. Under-represented environments can be identified for inclusion in a larger conservation unit. These environmental analyses can also be coupled with other conservation guidelines for conserving genetic diversity, such as conserving species on either side of a biogeographic barrier (Moritz, 2002).

It is important to point out that species distribution models presented here represent only hypotheses of historical and present-day occurrences, and field testing is needed to verify the accuracy of these models. Yet such verification will be hard to accomplish given the large changes in forest cover in the region. For example, how does one interpret the absence of a species in a patch predicted to be suitable for occupancy? Does this mean that the model is inaccurate, or might the population have gone extinct from this patch due to deterministic or stochastic processes? Nonetheless, our study was not designed to produce specific conservation recommendations, nor did we evaluate landscape connectivity and population viability. Rather, we highlight the importance of evaluating environmental niches of species or habitats historically and incorporating this information, when possible, into conservation planning and decision-making. If certain types of environmental conditions have become rare as a result of deforestation it may be advisable to consider these when designing conservation areas for future biological diversity. To this end, future reserves should not only conserve environmental conditions currently common in a species range but, when possible, those that have been common historically. This strategy should result in effective conservation of environmental surrogates of intra-specific diversity.

The persistence of many species in the Atlantic forests of Brazil, not only the currently globally threatened species, will probably depend on active management to restore habitats and increase connectivity to better represent and maintain the range of forest environments frequented by the region's species (see also Harris & Pimm, 2004; Harris *et al.*, 2005; Machado & Fonseca, 2006). In this study we did not project models of species distributions into future climates. However, given the expected significant changes in forest environments, which include novel environments that are warmer and less seasonal, the area occupied by species in this biodiversity hotspot will decline even further unless species are able to adapt to these new conditions or restoration efforts are both targeted and extensive.

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SUPPORTING INFORMATION

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

Figure S1 Comparison of environmental variables between 'historical' (pre-deforestation) and current forest cover (post-deforestation) in the Atlantic forest ecosystem of Brazil.

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BIOSKETCH

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