BIODIVERSITY RESEARCH

Biodiversity and land-use change: understanding the complex responses of an endemic-rich bird assemblage

Ricardo Faustino de Lima[1]*, Martin Dallimer[2], Philip W. Atkinson[3] and Jos Barlow[1]

[1]*Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK,* [2]*Forest & Landscape and Center for Macroecology, Evolution and Climate, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark,* [3]*British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK*

ABSTRACT

Aim Anthropogenic land-use change is a major driver of the current extinction crisis, but the processes through which it acts on biodiversity are complex and still poorly understood. Here, we use several biodiversity metrics to make a comprehensive assessment of the response of an endemic-rich bird assemblage to land-use change.

Location São Tomé Island (São Tomé and Príncipe, Africa).

Methods We sampled bird assemblages in 220 point counts, stratified across three regions and four land-use types. Species richness was examined using accumulation curves and generalized linear mixed-effect models. Compositional and structural changes were analysed with ordination techniques. We used correlations and model selection to identify species traits and environmental variables associated with such changes.

Results At the point level, there was a slight decrease of species richness in more intensive land uses. However, higher dissimilarities within these land uses led them to have higher overall species richness. Endemics dominated forest environments and, although most preferred less-disturbed land uses, many persisted across all land uses. Non-endemics were virtually absent from forests, but became very abundant in the more intensive land uses. Canopy cover was the best predictor of the shift between endemic and non-endemic species, and allowed identifying regional differences in the local responses of bird assemblages to land-use change.

Main conclusions To better understand biodiversity, it is crucial to use several metrics simultaneously. In São Tomé, simply using species richness, the single most used biodiversity metric, could have been misleading as it concealed major shifts in the bird assemblage structure towards an endemism impoverished avifauna. Despite scarce data on land-use cover, we demonstrate how landscape context can be vital to understand biodiversity patterns and that highly forested surroundings might overestimate the strict value of more intensive land uses. Our results raise concerns about the long-term persistence of endemic species restricted to islands where forested land uses are being lost.

Keywords

assemblage composition and structure, biodiversity loss, landscape context, São Tomé island, species richness, tropical forest.

*Correspondence: Ricardo Faustino de Lima, Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK. E-mails: r.delima@lancaster.ac.uk; rfaustinol@gmail.com

INTRODUCTION

Anthropogenic land-use change has caused a widespread loss of habitat and is widely recognized as the major driver of the ongoing biodiversity crisis (Myers *et al.*, 2000; Brooks *et al.*, 2002; Vié *et al.*, 2009). Most land-use change is driven by agriculture, and increasing demand for further agricultural products is raising concern about the future of biodiversity

(Tilman *et al.*, 2002; Green *et al.*, 2005; Phalan *et al.*, 2011). In this context, the future of tropical forests is of particular concern as they are the planet's most diverse terrestrial ecosystem (Myers *et al.*, 2000) and also one of the most threatened habitats, at the frontier of agricultural expansion and under fast increasing human influence (Laurance, 1999; Tilman *et al.*, 2001; Defries *et al.*, 2004; Bradshaw *et al.*, 2009).

Understanding how to minimize the impact of land-use change on biodiversity has become a major research objective in applied ecology, but the complex responses of biodiversity have often hindered progress (Lindenmayer *et al.*, 2008; Norris, 2008; Scherr & McNeely, 2008). Despite remarkable effort, we remain limited in our ability to address complex matters such as edge and scale effects, lack of congruence between taxonomic groups, while many studies suffer from methodological weaknesses relating to sampling design, biodiversity metrics or habitat categorization (Ewers & Didham, 2006; Barlow *et al.*, 2007; Gardner *et al.*, 2009). Differences between studies complicate the development of any general rules that could be applied to improve the persistence of biodiversity in human-modified land uses (Gardner *et al.*, 2009; Putz & Redford, 2010; Keith *et al.*, 2011).

Island ecosystems are particularly relevant for biodiversity conservation. They hold a disproportionately high number of unique (endemic) terrestrial species that simultaneously are prone to extinction driven by land-use change (Ricketts *et al.*, 2005; Kier *et al.*, 2009; Maas *et al.*, 2009; Waltert *et al.*, 2011). Their well-defined boundaries and simplified ecosystems mean that islands can also provide a good experimental setup to understand biological processes (Darwin, 1859; MacArthur & Wilson, 1967; Wardle *et al.*, 1997; Gillespie *et al.*, 2008). To study the effects of land-use change on biodiversity, birds are amongst the best taxonomic groups; they are diverse, well studied and cost-effective to sample (Furness & Greenwood, 1993; Barlow *et al.*, 2007; Gardner *et al.*, 2008; Kessler *et al.*, 2011). Several recent studies have looked at the effect of land-use changes on island avifauna, but most had some sort of constraint that did not allow providing a comprehensive assessment, as they focussed on a particular set of species (e.g. Sodhi *et al.*, 2005), used over-simplistic biodiversity measurements (e.g. Beukema *et al.*, 2007) or concentrated on relatively small areas of the island (e.g. Waltert *et al.*, 2004). Furthermore, results are often inconsistent from site to site (e.g. Waltert *et al.*, 2005). This suggests that the responses of insular bird assemblages to land use are highly context dependent, meaning such responses are governed by factors that remain poorly understood and that might have been overlooked.

Here, we examine the impact of land-use change on the endemic-rich bird assemblages of the tropical island of São Tomé. Although a few studies have focused on the island's bird assemblages (Atkinson *et al.*, 1991; Rocha, 2008; Dallimer *et al.*, 2009), this study represents the first island-wide systematic examination of the bird assemblages across land uses. Specifically we will examine: (1) how endemic and non-endemic bird species richness changes between land uses

at three distinct scales (island, region and sampling point); (2) how bird assemblage composition and structure change between land uses; (3) how endemism, body size and feeding guild relate to species' response to land use; and (4) which environmental variables best explain changes in the proportion of endemics.

METHODS

Study area

The Democratic Republic of São Tomé and Príncipe consists of two small oceanic islands located in the Gulf of Guinea (Central Africa 0°01′08″–0°24′27″N, 6°27′43″–6°45′39″E – Fig. 1), which have a widely recognized high degree of endemism across many taxa (Jones, 1994; Serrano, 1995; Measey *et al.*, 2007; Figueiredo *et al.*, 2011). The degree of endemism within the avifauna is particularly notable (Collar & Stuart, 1988; Buchanan *et al.*, 2011): of 45 resident terrestrial species, 17 are single-island endemics, three are endemic to the Gulf of Guinea oceanic islands (Annobón, São Tomé and Príncipe) and eight are widespread species represented in the
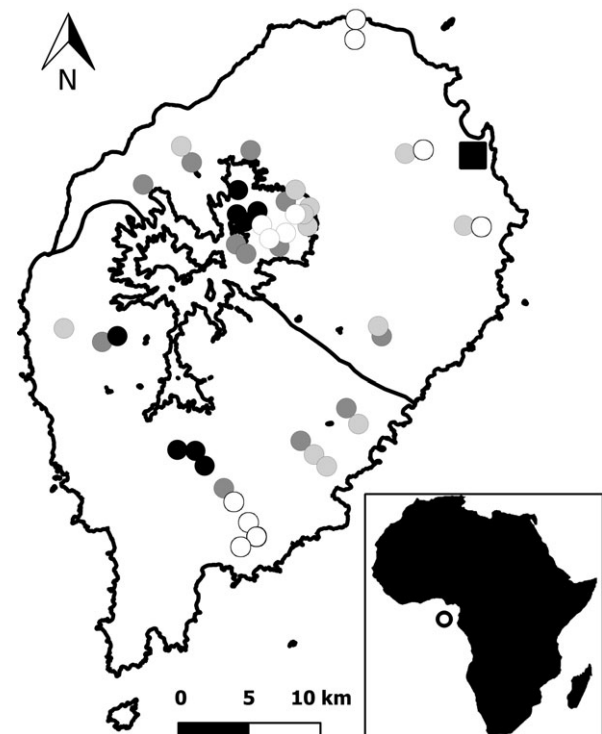

Figure 1 Map of São Tomé. The inset in the bottom right shows the location of the island in Africa (hollow dot). The contour lines are showing the three sampling regions: Montane (between 800- and 1400-m a.s.l.), North (up to 800-m a.s.l. and less than 2000 mm of annual rainfall) and South (up to 800-m a.s.l. and more than 3000 mm of annual rainfall). Each dot in the main map represents a transect, which is coloured according to the land use sampled: black – old-growth forest; dark grey – secondary forest; light grey – shade plantation; and white – non-forested. The capital, São Tomé, is signed by a black square.

island by an endemic subspecies (Table S1 in Supporting Information). Jones & Tye (2006) argue that the lack of early records for most of the 17 non-endemic species suggests that many might be recent arrivals at São Tomé. Additionally, these include species that are customary cage birds that would not have appropriate habitats prior to 1497, when Portuguese navigators first discovered the island, completely forested and with no permanent human settlements (Eyzaguirre, 1986).

The human occupation of São Tomé is fairly recent and, apart from some small coastal areas, most of the island is reported to have been almost untouched until the middle of the 19th century. At this point in history, most of the lowland forests and some montane forests were replaced by coffee and cocoa plantations, and only inaccessible and wet areas of south-west and central São Tomé remained covered by relatively undisturbed forest. Nowadays, this well-preserved forest block is buffered by secondary forest, resulting from logging and plantation abandonment. This, in turn, is predominantly surrounded by active shade plantations. Scattered around these, there are several non-forested land uses (Jones *et al.*, 1991; Diniz *et al.*, 2002). Forest inventories conducted in 1989 and 1999 estimated that around 90% of the island was still covered by forested land uses, with primary forest, secondary forest and shade plantation covering similar proportions of the island. However, there was a decrease of primary forests and shade plantation in the 10-year period between inventories, and an increase in the cover of secondary forests and non-forested land uses (BDPA, 1985; Salgueiro & Carvalho, 2001).

São Tomé has a complex landscape composition, holding very diverse land uses in a small area and in a highly intricate matrix of fragments with distinct shapes, sizes and history of human use. Although the understanding of such complexity is hindered by the lack of precise geographic information, this is not unusual: biodiversity with conservation importance often occurs in landscapes that do not allow ideal sampling designs, nor have good baseline information. However, São Tomé also has several characteristics that make it a good study case. It has land uses with very distinct degrees of intensification crossing strong natural environmental gradients, including unusually well-preserved insular forests that hold a remarkably high proportion of endemics and guarantee that these habitats have had little human influence, thus constituting a reliable reference situation. It also benefits from the existence of forestry inventories, which facilitate land-use categorization and allowed some level of landscape contextualization.

Experimental design

We divided the island into three sampling regions: Montane, delimited by the 800-m and 1400-m a.s.l. altitudinal ranges, which define a distinct forest type (Exell, 1944); North, comprising dry lowlands (annual rainfall under 2000 mm); and South, limited by the 3000-mm annual rainfall isohyet (Holdridge, 1947; Silva, 1958). Within each region, we defined four transects per main land-use category. To estimate the coverage of each land use and being able to analyse landscape context, we followed the forestry inventory's four broad land-use categories (INTERFOREST AB, 1990; Salgueiro & Carvalho, 2001). These were in order of increasing anthropogenic influence: old-growth forest, secondary forest, shade plantation and non-forested habitats. We therefore aimed to have four replicate transects in each of the four land uses, replicated across three regions ($n = 48$). However, old-growth forest in the North was too fragmented and could not be sampled effectively (Fig. 1), which lead to a total of 44 transects. Within each transect, we sampled birds at five point locations, separated by between 200 and 250 m (220 points in total).

In old-growth forest, the native flora dominates and there is no recent history of plantation or heavy logging. This forest typically has a high diversity of Orchidaceae and Pteridophyta, and a high proportion of endemic tree species (notably Rubiaceae and Euphorbiaceae), although invasive exotic plant species might be present (e.g. *Cinchona ledgeriana*, *Persea americana*, *Cecropia peltata*). Secondary forests have established as a result of agricultural abandonment or following recent tree felling for wood or charcoal. Here, both endemic and large trees are rare, while non-endemic low-quality wood trees dominate (e.g. *Artocarpus altilis*, *Erythrina poeppigiana*, *Celtis gomphophylla*). Shade plantation refers to agroforestry areas that have crops growing under the canopy of trees; the most typical systems are cocoa (*Theobroma cacao*) or coffee (*Coffea* sp.), intercropped with banana (*Musa* sp.) and taro (*Colocasia esculenta*), and shaded by coral trees (*Erythrina* sp.) and other species, which often provide food, wood or medicine to humans. The non-forested category includes biomes actively managed by people, but in which there are no crops growing under the cover of trees. These include a diverse range of different man-made habitats, predominantly oil palm monocultures, artificial savannahs and smallholder horticultures (Diniz *et al.*, 2002).

Point count characterization and avifaunal sampling

The coordinates of each point were taken by GPS (Garmin GMAP 76Cx). Vegetation measurements were made within a circular plot of 0.05 ha around each point, corrected for slope (Husch *et al.*, 2003). For each plot, we calculated canopy cover, understorey cover, tree species richness, canopy height and total basal area. Canopy cover was estimated by averaging readings of canopy cover taken in the four cardinal directions and five steps away from each point count, using a convex spherical densiometer. The proportion of understorey cover in each plot was assigned to one of five categories: 0–0.2, 0.2–0.4, 0.4–0.6, 0.6–0.8 and 0.8–1. Canopy height was obtained as the height of the tallest tree, measured with a declinometer. To calculate total basal area, we measured diameter at breast height (d.b.h.) of all plants with a d.b.h. greater than or equal to 10 cm and summed each tree's basal area.

Bird assemblages were sampled during the dry seasons (from the middle of May until the end of August) of 2009 and 2010, with at least 2 weeks separating repeated counts at the same transect within each year. To make sure that there was no observer bias between point counts, each of the 220 sampling points was surveyed three times, once by each of three experienced observers. We counted the number of individuals of all species that were detected visually or aurally during 10-min point counts. Observations beyond 20 m from the point count were excluded to ensure that birds from adjacent land uses were not inadvertently sampled, especially in the more fragmented landscapes. This exclusion helped to assure independence between sampling locations, but did not allow us to apply methods that account for detectability, such as distance sampling (Buckland *et al.*, 2001) or occupancy modelling (MacKenzie *et al.*, 2002). Instead, we consider that all birds within this radius were detected, an assumption we argue is reasonable for a 20 m radius. Counts took place in the morning, between 05:40 h and 11:00 h, to maximize detection and, whenever possible, sampling was rotated to assure that the same point would be sampled at different times.

Data analysis

We used Tukey tests for generalized linear mixed-effect models (GLMMs) to compare the number of species detected per point count between land uses. Using EstimateS v. 8.0 (Colwell, 2006), we calculated first-order jackknife, to estimate the total species richness of each land use, and built sample-based rarefaction curves, to compare species richness across land uses (Gotelli & Colwell, 2001). We repeated all these analyses with only endemic and only non-endemic species (endemic subspecies included in the latter) and also built sample-based rarefaction curves for each region (Montane, North and South).

We analysed changes in the composition of the bird assemblage between land uses by identifying species that did not occur in all land uses. We conducted an indicator species analysis using abundance data – number of individuals detected per sampling unit – in PC-ORD 5.0 (McCune & Mefford, 1999), which allows us to identify species associated with each land use (Dufrene & Legendre, 1997). Differences in the bird assemblage structure were then explored using non-metric multidimensional scaling (NMDS) plots based on the Bray–Curtis similarity index, using log-transformed and standardized abundance data. As each point count was only sampled three times, we used the data per transect to ensure that the levels of sample representation were high enough to make meaningful comparisons of assemblage structure. To measure and test differences in bird assemblages between land uses, we used SIMPER and one-way ANOSIM, respectively. We repeated these analyses using only the data for the endemic species. Subsequently, we used NMDS to understand how species were grouped in terms of occurrence in the different transects (ordinating species rather than transects). Finally we used Spearman's rank correlation coefficient to evaluate the correlation between the two main ordination axes and the species traits (ende-mism, feeding guild and body size). NMDS, SIMPER and ANOSIM were undertaken in Primer 5.2.4 (Clarke & Warwick, 2001).

We assessed the influence of vegetation on the proportion of endemic bird species, using GLMMs that included the land-use type, region and all vegetation variables (canopy cover, understorey cover, forest basal area, tree species richness and canopy height), accounting for the nested sampling design (points within transects). To identify which variables best explained the proportion of endemic bird species, we used model selection based on Akaike's information criterion corrected for small samples sizes (AICc – Burnham & Anderson, 2002; Barlow *et al.*, 2010). Unless otherwise stated, statistical procedures were carried out in R v. 2.10.0 (R Development Core Team, 2009).

RESULTS

During 660 10-min counts, we registered 4091 individuals of 33 bird species. 77.2% of observations were of 16 endemic species (Table S2).

Species richness – endemics and non-endemics

The average number of species detected per point count was only significantly different between secondary forest and non-forested land uses, with the last being poorer (Fig. 2a and Table S3). Non-forested land uses were significantly poorer in endemic species than all other land-use types, while for non-endemics, the number of species increased with land-use intensity, not being significantly different only between secondary forest and shade plantation (Fig. 2b and 2c and Table S3).

At the land-use level, both recorded and estimated species richness increased from the least to the most intensive land use. The number of species was significantly different between all land uses, except between old-growth and secondary forests and between secondary forest and shade plantation (Fig. 2d and S1a). When considering endemic species only, the differences between land uses were exactly the same, but the rank of species richness was completely reversed with forests being the most species-rich land uses (Fig. 2e and Fig. S1b). For the non-endemic birds, more intensive land uses had consistently and significantly more species than the less intensive ones (Fig. 2f and S1c). These island-wide patterns of total, endemic and non-endemic species richness were consistent across each of the three regions considered, although differences between land use tended to be attenuated within regions. It was also noticeable that fewer endemic species persisted in the non-forested land uses in the North, and that, in the South, there were less non-endemic species even in intensive land uses (Fig. S2).

Changes in bird assemblage composition across land uses

The indicator species analysis illustrates a shift, with the endemic birds associated to the forested land uses and the
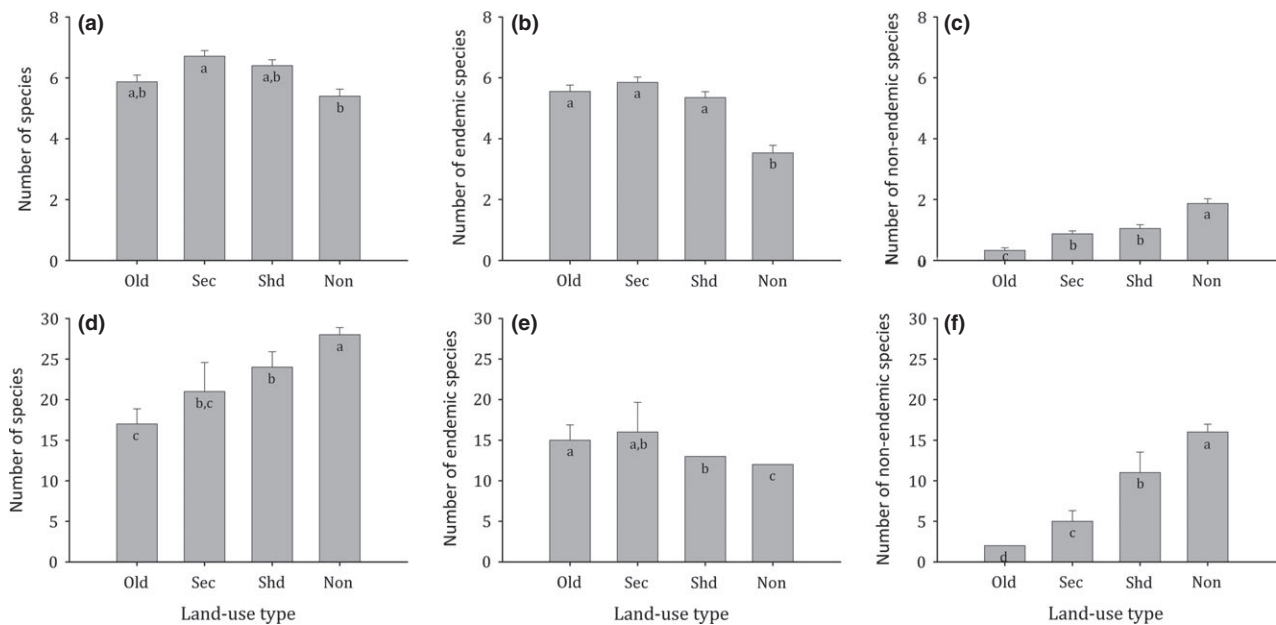
Figure 2 Species richness across land uses, at the point (a–c) and at the land-use level (d–f). At the point level, values represent averages and error bars represent standard error (Table S3). At the land-use level, the number of species was taken from sample-based rarefaction curves (Fig. S1). Small-case letters indicate groupings, with the alphabetical order indicating significantly lower species richness. Across land use, differences in species richness were evaluated at the point level using Tukey tests for GLMMs with a 95% confidence interval, and at the land-use level from the sample-based rarefaction curves.

non-endemic to the non-forested (Fig. 3 and Table S4). Of the 33 bird species recorded, 14 occurred in all land uses. Of these, 12 were endemic species and two were endemic sub-species, the chestnut-winged starling *Onychognathus fulgidus fulgidus* and the lemon dove *Columba larvata simplex*. The remaining endemic species detected were scarce (maroon pigeon *Columba thomensis* and São Tomé scops owl *Otus hartlaubi*) or restricted to forest (giant sunbird *Dreptes thomensis* and São Tomé oriole *Oriolus crassirostris*). The red-headed lovebird *Agapornis pullarius*, the common waxbill *Estrilda astrild* and the black kite *Milvus migrans* were the only non-endemic taxa registered within forests, and none of them were recorded in old-growth forest. The endemic sub-species of vitelline masked weaver *Ploceus velatus peixotoi* was recorded in shade plantation and in non-forested land uses, together with five other non-endemics, while the endemic subspecies of harlequin quail *Coturnix delegorguei histrionica* and the remaining five non-endemics were only recorded in non-forested land uses (Fig. 3 and Table S2).

Changes in bird assemblage structure

Despite the large proportion of species that persisted across all land-use categories (14 of 33), there were significant differences in the structure of bird assemblages between land uses, and only old-growth and secondary forests were not significantly different from each other (Fig. 4 and Table 1). The first two axes of the NMDS had a stress value of 0.13, indicating that our data were well represented in these two dimensions. The most intensive land uses also tended to

have a lower similarity between transects. These patterns persisted for the endemics-only analysis, but assemblage similarity was enhanced both between and within land-use type (Table 1). The similarity of the bird assemblages was partially explained by the geographic distance between sites (Spearman's rho = 0.27, P < 0.001).

To complement the ordination of transects, we ordinated species according to their abundance in transects (Fig. 5). The first two axes of the NMDS had a stress value of 0.11, again indicating that two dimensions were enough to give a good representation of our data. Endemics were clearly separated from non-endemics (Fig. 5a). The more abundant species were concentrated in the centre of the plot, while the rare and land-use sensitive endemics or localized and scarce non-endemics were more dispersed, indicating that most of the assemblage differentiation between transects was due to the less abundant species. Size and feeding guild were correlated with differences in the assemblage structure: larger-bodied and frugivore birds preferred less intensive land uses, while small granivore species preferred most intensive land uses (Fig. 5b).

Do the vegetation characteristics predict the proportion of endemic species?

Canopy cover, canopy height, forest basal area and tree species richness all had positive effects on the proportion of endemic bird species, while land-use intensity had a negative effect and understorey cover a variable influence depending on the specific model. Canopy cover was the strongest predictor of the proportion of endemic species in the point
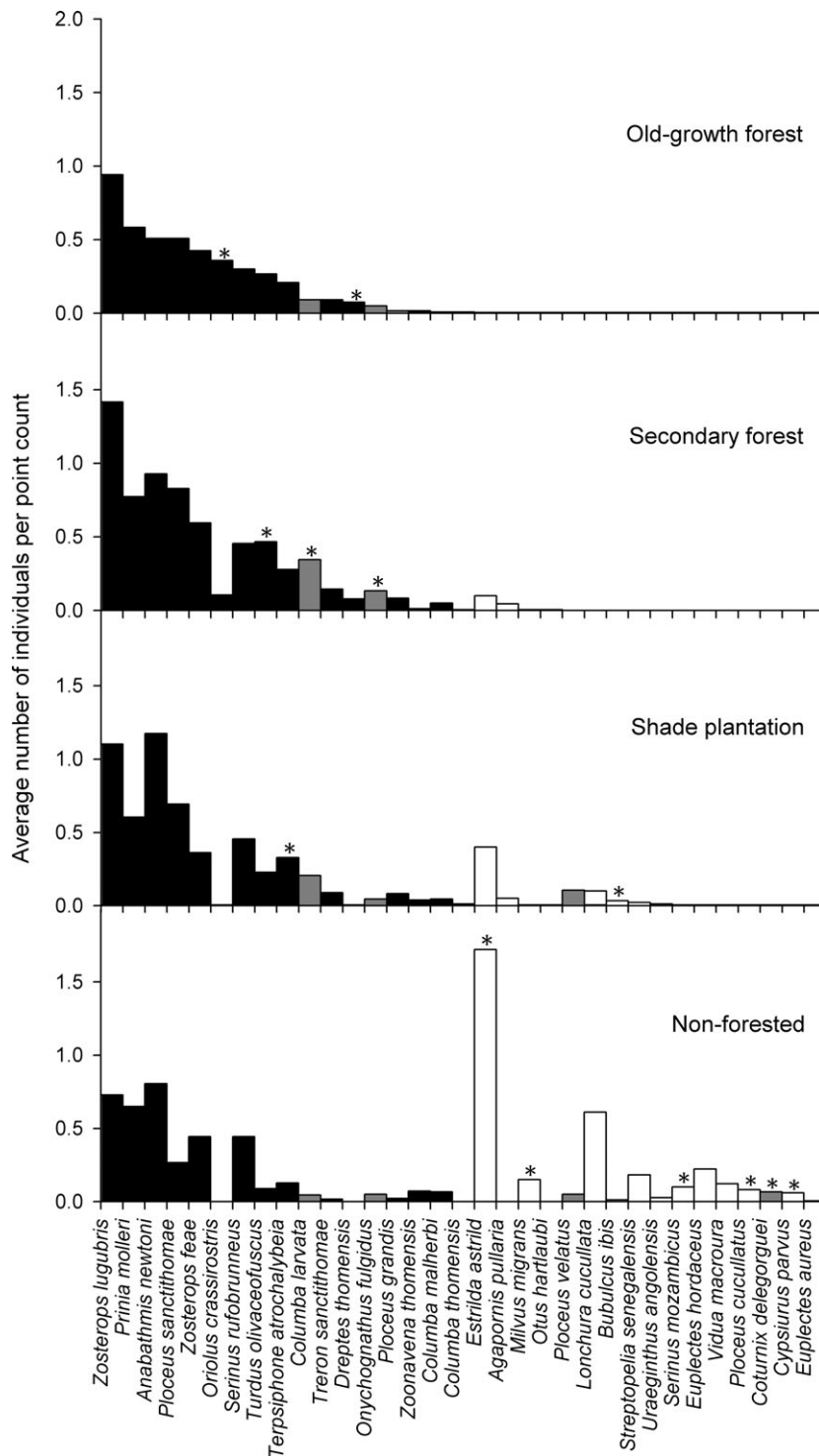
Figure 3 Species abundance across land uses. The average number of individuals recorded from each species in a point count after three visits is shown by land use type. Species are ranked according to the abundance in the less intensive land use where they occur (old growth if present, or the subsequent if absent from old growth). Black bars denote endemic species, grey bars endemic subspecies and white bars non-endemics. Asterisks denote the indicator species ($P < 0.05$ – Table S3).

counts; it was the only variable included in the best model, it was present in all of the 19 top models and its inclusion always increased model performance (Table S5). The best model suggests that the relationship between canopy cover and the proportion of endemics differs between regions; to have more than 80% of endemic bird species in a point count, as obtained for more than 95% of the point counts in old-growth forest, 45% and 57% of canopy cover are

enough in the Montane and South regions, respectively, but 80% is needed in the North (Fig. 6). The strong link between canopy cover and the proportion of endemics is due to the combined positive effect of canopy cover on endemic species richness and negative influence on non-endemic species richness. It is also worth noticing that the relationship between canopy cover and the number of endemic bird species is weaker (Spearman's rho = 0.30,
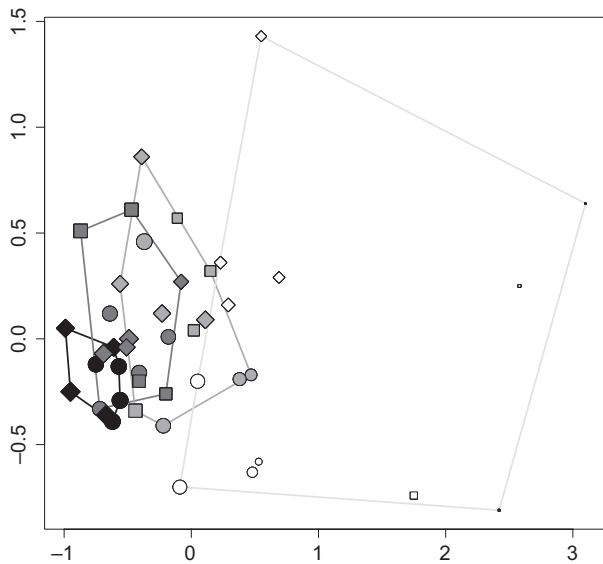
Figure 4 First two axes of the non-metric multidimensional scaling (NMDS) ordination of bird assemblages across the transects. The stress value of this analysis was 0.13. The sample scores are shown, with colour representing the type of land use (black – old-growth forest; dark grey – secondary forest; light grey – shade plantation; white – non-forested), size, the proportion of endemic species and shape, the region (circle – Montane; square – North; losang – South). Transects within same land use are grouped by the minimum convex polygon.

$P < 0.001$) than between canopy cover and the number of non-endemics (Spearman's rho = -0.42, $P < 0.001$) and that there is no clear influence of canopy cover on total species richness (Fig. S3).

DISCUSSION

In this study, we looked at the impact of land-use change on the endemic-rich bird assemblages of the tropical island of São Tomé and observed an increase of species richness associated with land-use intensity. However, this increase was due to a rise in the number of non-endemic species, and endemic species richness tended to decrease in more

intensive land uses. The composition and structure of the bird assemblages differed between land uses, with endemic, frugivorous and larger species being significantly impaired by the increasing land-use intensity. We show that canopy cover is the variable that best explains the shift from endemic-dominated to endemic-impoverished bird assemblages, but that its influence varies between regions, suggesting a strong effect of landscape context on the response of bird assemblages to local variables.

Land-use intensification: When more is less

During the point counts, we recorded 33 bird species, 16 of which were endemic (from a total of 20 Santomean endemics). Most of these endemics persisted across land uses, but the bird assemblages still changed significantly. Despite having lower point species richness (Fig 2a), the non-forested habitats present the highest species richness at the transect level (Fig. 2d). This apparent discrepancy can be explained by an increased dissimilarity between point counts in more intensive land uses (Fig. 4), which in turn is linked to a higher number of non-endemic species and conceals the decline of the endemics (Figs. 2). Previous studies have also reported higher richness in disturbed habitats (Sodhi *et al.*, 2005; Almeida *et al.*, 2011). Following the habitat-heterogeneity hypothesis (Cardinale *et al.*, 2000; González-Megías *et al.*, 2011), this might be related to an increased environmental variability in these land uses. Despite having higher species richness, more intensive land uses tend to hold an avifauna that is less unique (McKinney & Lockwood, 1999), and therefore, forests remain of higher conservation interest. These results show that species richness can be an uninformative and misleading biodiversity indicator of conservation value and that it should be complemented by other metrics.

Non-endemic species clearly preferred disturbed land uses (Fig. 3), and mostly as a result of that, the proportion of endemic bird species declined with increasing land-use intensity (Fig. 3, and Tables S2 and S4). Endemic species that were abundant in the forests tended to persist in more intensive land uses. Thus, differences in assemblage structure were mainly attributed to changes in the abundance of the

Table 1 Across land-use comparison of the bird assemblage structure for all species and just endemics. The values were obtained by SIMPER analysis and represent the similarity of transects within land use (diagonal) and the dissimilarity between land uses (top right). The levels of significance obtained with one-way ANOSIM are shown on the bottom left of each table (Global $R = 0.29$, $P < 0.001$ for all species and Global $R = 0.20$, $P = 0.001$ for the endemics)

	All species				Endemic species			
	Old	Sec	Shd	Uns	Old	Sec	Shd	Uns
Old-growth (Old)	*77.99*	28.02	35.91	53.25	*81.01*	24.31	28.45	38.39
Secondary (Sec)	n.s.	*71.77*	32.45	50.46	n.s.	*75.09*	24.83	34.92
Shade (Shd)	***	**	*67.23*	46.53	***	n.s.	*76.52*	32.61
Unshaded (Uns)	***	***	***	*51.86*	**	**	*	*62.43*

ANOSIM significance: n.s., 0.05; *<0.05; **<0.01; ***<0.001. Values in italic were not tested and therefore there are no associated levels of significance.
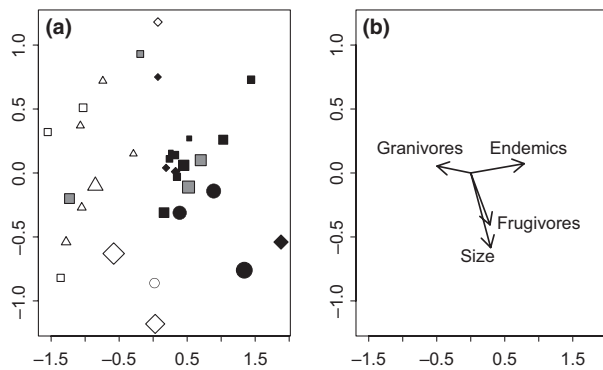
Figure 5 (a) Non-metric multidimensional scaling (NMDS) of bird species, according to their abundance across the transects. The stress value of this analysis was 0.11. The colour represents the level of endemism (black – endemic species; grey – endemic subspecies; white – non-endemic), size represents the average weight of the species and shape represents the feeding guild (circle – frugivore; square – omnivore; losang – carnivore; triangle – granivore). In (b), the arrows indicate the species traits that have significant correlations with the two main ordination axes (Spearman rho, *P*-value < 0.05).

non-endemics and of the least abundant endemics (Figs 3 & 5). The only non-endemic species that ordinated within the cluster of endemic species were the endemic sub-species of lemon dove and chestnut-winged starling, which are morphologically very distinct from the continental individuals (Atkinson *et al.*, 1994; Leventis & Olmos, 2009).

Trait shifts associated with land-use change

In island systems, there is a limited pool of species available to colonized disturbed areas. Within São Tomé, these areas were occupied by an array of species thought to have been introduced during the colonial period (Jones & Tye, 2006). These include many of the small granivorous bird species that replace the larger, endemic and frugivorous birds characteristic of less intensively managed habitats (Fig. 5). The change in feeding guilds suggests that bottom-up restrictions such as habitat and resource limitations (e.g. food availability) may have had an important role in creating the differentiation of bird assemblages observed between land uses in São Tomé. However, more intensive land uses also tended to be more visited by people, and therefore, direct top-down anthropogenic actions, such as hunting, might be important, especially as large frugivore birds are more sensitive to direct human pressures than small granivore species (M.B. Carvalho, 2008, unpublished data). The introduction of numerous non-avian species (e.g. pig *Sus domesticus*, cat *Felis catus*, black and brown rats *Rattus* sp., mona monkeys *Cercopithecus mona*) is likely to play an important role in modelling the bird assemblage structure along the different land uses (Atkinson, 1996). Given the originally depauperate theriofauna of São Tomé (Dutton, 1994; Wiles *et al.*, 2003), it is likely that these introduced species have overall negative impacts on the bird assemblage. Nevertheless, it is difficult to estimate their impact; little is known about their ecology in São Tomé, each species has a different distribution along the land-use types and no land-use type is free of these species.

Variations in bird assemblages: the role of local and landscape characteristics

Most characteristics of the vegetation, and particularly the canopy cover, were positively correlated with the proportion of endemic species registered in each point count. Forest degradation simultaneously drives a decline in the number of endemics and a rise in the number of non-endemic species (Fig. S3). The latter responds more directly to the loss of
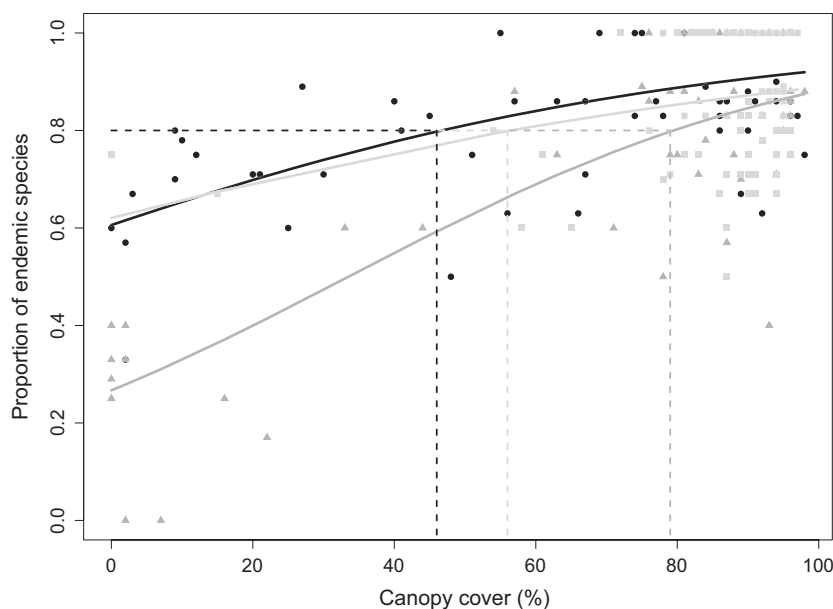

Figure 6 Effect of canopy cover on the proportion of endemic species. The dots represent the values observed in the different regions. The continuous curved lines represent the generalized linear models, while the dashed lines show the canopy cover retrieved by each model for a proportion of four-fifths of endemic species. Regions are distinguished by colour and dot shape: black circles – Montane; dark grey triangles – North; and light grey squares – South.

canopy cover (compare Fig. S3a and S3b), so it could be that they are more responsive to local variables, while the endemics are mostly dependent on the existence of favourably forested habitats at the landscape level (Dias, 1996; Mouquet & Loreau, 2003; Zurita & Bellocq, 2010). Although adequately testing this hypothesis would require more data, the observed difference between regions seems to be congruent with it; the pervasiveness of endemic species into areas with less canopy cover falls more abruptly in the forest-depauperate North than in the highly forested Montane and South regions (Fig. S3a). Considering these indications of a 'spillover' effect and the short history of human presence on the island, the current biodiversity value of anthropogenic land uses might be overestimated. If so, further land-use intensification will not only decrease the value of any land use for the endemic species locally, but act pervasively across the landscape.

Land-use change and the future of São Tomé's endemics

Our results confirm previous suggestions that land-use change is a major threat to the persistence of São Tomé's unique biodiversity (Atkinson *et al.*, 1991; Jones *et al.*, 1991). Despite the wide forest cover of São Tomé and the relatively high proportion of well-preserved forests remaining (roughly one-third of the island), there is reason for concern. The proportion of endemic species in the less forested North region is depauperate relative to the other more forested regions, even when local characteristics are favourable. This suggests that the current overall high prevalence of endemics in the agricultural matrix is linked to favourable landscape contexts. Under these circumstances, modifying the existing landscape configuration is expected to have strong negative effects on the endemic avifauna, acting pervasively across land uses (Dallimer *et al.*, 2009) and eventually leading to regime shifts (Pardini *et al.*, 2011), such as the replacement of an endemic-dominated by a non-endemic-dominated bird assemblage. Given the lack of across taxa congruence in response to land-use change (Barlow *et al.*, 2007) and the quick adaptability of birds to environmental changes (Furness & Greenwood, 1993), it is also likely that other Santomean endemic-rich taxa are more sensitive to land-use change than the birds.

Our knowledge of land-use changes in São Tomé is obscured by a lack of detailed information on past and present land uses, but several factors indicate that the pace of change is likely to be increasing towards more intensive uses. The country's socioeconomic setting has changed dramatically with the discovery of offshore oil reserves in the 1990s (Frynas *et al.*, 2003; Weszkalnys, 2009). The human population is growing very fast; from never having surpassed the 70,000 people until the 1970s, it is expected to pass the 200,000 mark by 2021 (Instituto Nacional de Estatística, 2009), thus reaching a population density identical to that of Italy. This boom has already had a measurable impact on forestry resources (Salgueiro & Carvalho, 2001).

Concluding remarks

Species assemblages can have very complex responses to land-use change. Our work has shown that the loss of forest to agricultural land uses has deleterious effects on São Tomé's endemic avifauna, but that, paradoxically, more intensive land uses also had higher species richness. Ordination analyses proved to be more sensitive to change in the bird assemblage than the mere number of species. These results support the importance of distinguishing different subgroups of species and using multiple metrics in biodiversity analyses. We showed that the endemics persisted best in regions that were more forested, and thus the importance of landscape context in shaping biodiversity, even in the absence of detailed spatio-temporal data on land-use cover. Finally, our results highlight that human-modified forested land uses, including secondary forests and shade plantations, can hold significant numbers of island endemics. This goes against the general assumption that island endemics are inherently sensitive to human interference, and instead suggests that it might be the ease in completely converting many island ecosystems into humanized landscapes, which has caused the extinction of so many island species. Taking into account our findings, we advise against land-use intensification involving the loss of canopy cover or the reduction in the proportion of forested land uses in São Tomé, or in other endemic-rich small islands that were originally covered by forest ecosystems.

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SUPPORTING INFORMATION

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

Figure S1 Sample-based rarefaction curves for a) all species, b) just endemics and c) just non-endemics across land-uses.

Figure S2 Sample-based rarefaction curves for all (a-c), endemic (d-f) and non-endemic (g-i) species across the different land-uses and regions: Montane (a, d and g), North (b, e and h) and South (c, f and i). Small-dotted lines show the 95% confidence intervals.

Figure S3 Effect of canopy cover on the endemic (a), non-endemic (b) and total (c) number of species.

Table S1 Characteristics of the bird species detected during the point counts.

Table S2 Bird species' observed abundance and frequency.

Table S3 Average number of species detected per point count across land uses.

Table S4 Results of the indicator species analysis.

Table S5 Models for explaining the proportion of endemic species per point count, ranked for AICc values.

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BIOSKETCH

Ricardo Faustino de Lima is a PhD student at Lancaster University (2008–2012). He has a wide interest in ecology and particularly in the application of scientific knowledge to halt the loss of biodiversity. He has worked mostly on birds, with his current research focusing on the effects of land-use change and agriculture and forestry practices on the biodiversity of the endemism-rich island of São Tomé.

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