



The importance of novel and agricultural habitats for the avifauna of an oceanic island

Martin Dallimer^{a,*}, Mark Parnell^b, Jake E. Bicknell^c, Martim Melo^{d,e}

^a Division of Economics, Policy and Management Planning, and Center for Macroecology, Evolution and Climate, University of Copenhagen, Rolighedsvej 23, DK-1958 Copenhagen, Denmark

^b en:mapping, Mapping GIS & Spatial Solutions, Sheffield S6 3JS, UK

^c Durrell Institute of Conservation and Ecology (DICE), School of Anthropology and Conservation, University of Kent, Canterbury, Kent CT2 7NR, UK

^d Percy FitzPatrick Institute of African Ornithology, DST/NRF Center of Excellence, University of Cape Town, 7701 Rondebosch, Cape Town, South Africa

^e Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO/UP), Campus Agrário de Vairão, 4485-661 Vairão, Portugal

ARTICLE INFO

Article history:

Received 20 July 2010

Received in revised form 3 March 2012

Accepted 8 April 2012

Keywords:

Agriculture

Agroforestry

Distance sampling

Island species

Gulf of Guinea

São Tomé and Príncipe

ABSTRACT

Conservation management can no longer rely on protecting pristine habitats, but must consider the wider landscape. This is especially true on oceanic islands where endemic species are believed to be particularly susceptible to the extinction risks that accompany land conversion. Despite this, there is a paucity of studies examining how endemic communities on oceanic islands may be distributed across such human-modified habitats. Taking Príncipe Island in West Africa as a case study, we investigate how avian communities vary across the habitats (primary forest, secondary forest, agricultural areas) of this globally important centre of endemism. Here, recent policy reforms aimed at poverty alleviation and increased food production are rapidly altering the current land-use mosaic. Across all habitats, 27 bird species were encountered. Survey points in secondary forest and agricultural areas were, on average, more diverse and held higher overall abundances of birds than those within primary forest. This was true for both the entire avian assemblage and the endemic species alone. Nevertheless, two IUCN-listed species were restricted to primary forest, and many other endemics occurred at higher densities within this habitat. We demonstrate that agricultural areas and novel habitats, such as secondary forest, can hold high abundances of endemic species and thus have the potential to act as a resource for biodiversity conservation. A double-stranded approach to conservation is therefore required that both protects the integrity of the primary forest and controls the rapid changes in agricultural land-use to ensure that it continues to support a large component of the endemic avifauna.

© 2012 Elsevier GmbH. All rights reserved.

Introduction

Globally, the conversion of natural habitat continues apace for food and raw material production (Balmford et al. 2005; Field et al. 2008; Fitzherbert et al. 2008). The expansion of the agricultural sector remains a key threat to many IUCN-listed species (Green et al. 2005; IUCN 2010) and also to regions known to hold high levels of biodiversity (Buchanan et al. 2009). Hence conservation management can no longer exclusively rely on protecting pristine habitats, but must also consider the wider human-dominated landscape. Modified ecosystems such as those that are actively managed or that have fallen into disuse, are directly relevant for ecosystem service provision. There is a growing realisation that, under some circumstances, they may offer valuable habitats for biodiversity conservation (Gardner et al. 2009; Hobbs et al. 2006; Perfecto &

Vandermeer 2008). In those temperate regions where most of the land surface has already been appropriated for human use the role of agricultural landscapes for biodiversity conservation has been well studied (e.g. Benton et al. 2003; Butler et al. 2007; Mattison & Norris 2005). However, the most biodiverse systems are in the tropics (Myers et al. 2000), and it is these regions where human population growth, the conversion of natural habitats and extinction risks are at their highest (Cincotta et al. 2000; Vamossi & Vamossi 2008).

In tropical rainforest biomes, most research on the conservation potential of agricultural landscapes has focused on agroforestry (Bhagwat et al. 2008; Perfecto & Vandermeer 2008). These systems provide high levels of tree cover, diversity and vegetation structure and therefore have the potential to support some of the ecosystem functions and processes that are also found in primary forest (Steffan-Dewenter et al. 2007). For example, shade forest plantations of cacao and coffee are often considered to be important alternative habitats for rainforest species (Schroth et al. 2004; Schroth & Harvey 2007 and references therein). Indeed, previous

* Corresponding author. Tel.: +45 35 33 18 03; fax: +45 35 33 26 71.

E-mail addresses: mada@life.ku.dk, m.dallimer@gmail.com (M. Dallimer).

work has shown that agroforests can play a major role in the conservation of birds (e.g. Abrahamczyk et al. 2008) and other taxa (e.g. Bos et al. 2007; Perfecto et al. 2003).

Despite this research, less is known about the biodiversity conservation potential of novel ecosystems in tropical regions. In contrast to actively managed agricultural lands, a novel ecosystem or habitat is one that has been heavily influenced by people but is not under current human management and can be defined as “lands without agricultural or urban use embedded within agricultural or urban regions” (Marris 2009, p. 450). They are thought to represent around 35% of global land cover (Marris 2009) and, although generally considered to be the undesirable cousins of natural habitats, novel systems can maintain many of their functions (Hobbs et al. 2006). Although such habitats do have species compositions that have not previously occurred in a given biome (Hobbs et al. 2006), levels of biodiversity can be high, and can match (or exceed), that of native habitats (e.g. Mascaro et al. 2008). In general, however, a high proportion of this species richness comprises non-native, or even invasive, species.

An understanding of such novel, human-modified habitats is disproportionately important in centres of endemism, such as oceanic islands, which have often been subject to disproportionate amounts of human-driven habitat change (Diamond et al. 1989; Fordham & Brook 2010; Sadler 1999). Persistence of island endemics will therefore depend on their ability to adapt to human-modified habitats, with the expectation that those species that are specialists in pristine habitats are more likely to go extinct (Ricklefs & Bermingham 2002). Here we examine the impact of human-modified habitats on the resident landbird communities of Príncipe Island in the Gulf of Guinea, a globally important centre of endemism (Jones 1994; Jones & Tye 2006). Out of the 33 breeding landbirds (including the feral pigeon *Columba livia* and a likely extinct subspecies of olive ibis *Bostrychia olivacea*), there are eight single-island endemic species, three endemic species shared with the neighbouring island of São Tomé and seven endemic subspecies of mainland species (Jones & Tye 2006; Melo 2007). This level of bird endemism is at least double that found in most similar-sized islands worldwide (Melo 2007). Four of these species are IUCN-listed as either Vulnerable or Near-Threatened (IUCN 2010), whereas the recently described Príncipe Thrush (Melo et al. 2010) qualifies for the Critically Endangered category (Dallimer et al. 2010), and an as yet undescribed scops owl (*Otus* sp.) is a likely further addition to the endemic and threatened species list (Melo & Dallimer 2009). Despite such levels of endemism, little is known about the distribution, ecology and threats affecting many of the resident species (but see Dallimer & King 2008).

Historically, the island nation of São Tomé and Príncipe was a major producer of sugarcane (in the 16th Century) and the world's largest cocoa producer (in the early 20th Century). However, in the latter part of the 20th Century a large number of plantations were abandoned, leading to the present day expansion of secondary forest (for a detailed timeline see Jones & Tye 2006). This is particularly evident on Príncipe, where novel habitats, consisting of abandoned plantations and secondary forest, are the major land cover and form a mosaic with agriculturally productive land. The value of these habitats for the island's birdlife has never been quantified, although relative measures of occurrence suggest that the current situation is favourable to the endemic bird community (Jones & Tye 2006; Peet & Atkinson 1994). However, land use patterns are undergoing change as new agricultural and land ownership policies aimed at increasing food production and reducing poverty are implemented. Although this process has been relatively successful in improving livelihoods it has altered land use to the extent that the government of the islands regards finding a model of sustainable land-use as a high priority. Establishing a link between land use and the endemic landbirds of Príncipe is therefore urgently needed.

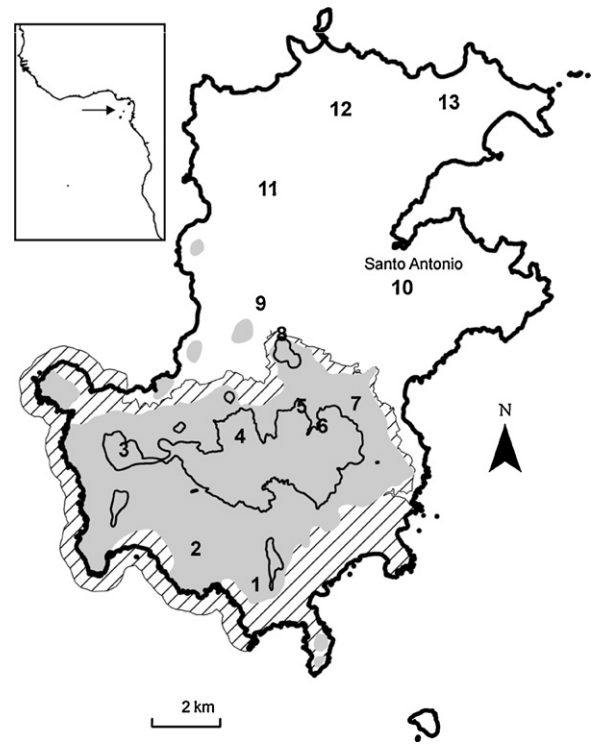


Fig. 1. Study sites for avian diversity and abundance on Príncipe Island, West Africa. The shaded area indicates the extent of primary forest, hatched area the extent of the Parque Natural d'Obô protected area, and the solid line the 400 m contour. Santo António, the only urban centre, is indicated. Inset gives the location of Príncipe in the Gulf of Guinea.

We provide the first quantitative study on the extent to which novel and agricultural landscapes are able to support the endemic landbird community on Príncipe Island. Our results will contribute to the further understanding of the ability of oceanic island endemic species to adapt to human environments, and will provide guidance for an agricultural policy able to sustain the large complement of endemic species. We examine the response of bird communities to both local and landscape-scale habitat and land-cover factors. Specifically, the following research questions were addressed: (1) to what extent are endemic bird species found in the human-modified habitats (secondary forest and agricultural areas) of the island? (2) what characteristics of (a) vegetation structure and (b) landscape context determine the abundance and richness of the avian assemblage?

Materials and methods

Study area

Príncipe (7°25'E 1°40'N; 139 km²), in the Gulf of Guinea, lies 220 km from the African coast and 146 km north of São Tomé. The north of the island is relatively flat and contains most of the human population, and current and abandoned agricultural land. The island is dominated by three main habitats: agricultural areas; secondary; and, primary forests. Agricultural areas feature low-intensity cocoa, fruit trees, maize and other subsistence crops. Significant tracts (approx. 41 km²) of primary and late secondary rainforest remain in the south and west of the island, which form the bulk of the 'Parque Natural d'Obô do Príncipe' protected area (Fig. 1). Here the terrain is more rugged and includes the highest mountain, Pico de Príncipe (948 m).

Study design

Thirteen study sites were visited in 2007, selected to cover three representative habitats on the island (Fig. 1). Six were within primary forest, three in secondary forest and four in agricultural habitats. Primary forest sites were further divided into those at low (up to 300 m), medium (to 500 m) and high (above 500 m) altitudinal bands (Table 2). At each study site, up to 21 survey points were placed with the intention of covering the range of available vegetation structures and local habitat variations found in the area. Survey points were separated by at least 150 m, a distance that was considered adequate by the observers to avoid double sampling the same areas of forest. To maximise the chances of encountering the highest number of species (Table 1) across Príncipe, field surveys, consisting of a single visit to each study site, were carried out during the period corresponding to the likely and known breeding seasons of resident birds (November and December; Dallimer et al. 2009, 2010; Jones & Tye 2006) and during the early morning.

Avian survey methods

To assess the occurrence and density of avifauna across the island, we employed a point-based method and used distance sampling to account for variation in the detectability of different species across habitats and according to the cue (visual/aural) used to locate birds (Thomas et al. 2010). This approach does not, however, account for failure to detect species that may have been present at a given point. In addition, many registrations were likely to be purely aural, but judging the location of singing birds in dense vegetation is known to be subject to error (Simons et al. 2007). Such errors were minimised here as the observers were already fully familiar with the species and habitats, and by using a laser rangefinder (Rangemaster LRF 800, Leica Camera AG, Germany) for distance measurement before assigning birds to one of three distance bands for later analysis (0–25, 25–50, over 50 m).

On arrival at a survey point, an initial five-minute settling-down period was used to note positions, identities and flock size of birds present. Thereafter, five minutes of actual survey time were allowed to measure distances, confirm locations and identifications. Birds solely flying over the points were excluded from density calculations. The short survey time of this method ensured that biases associated with birds moving in response to the observer were minimised. Nevertheless, it was not possible to identify reliably the two species of starling that occur on Príncipe (*Lamprolornis ornatus* and *L. splendidus*) in the field from their calls. We therefore recorded and analysed them together as 'starlings' throughout.

Bird densities were calculated using Distance software (version 5.0, release 2), which allows the variability in species' detectability to be incorporated into estimates of their density. Species-specific density functions were estimated for all species with 60 or more registrations. For less common species, a detection function was estimated using registrations for a group of similar species (here divided into passerines and non-passerines; Table 1). Whether covariates of detectability (habitat and/or cue type) were included and the final form of the detection function was decided according to minimum Akaike Information Criteria (AIC) and chi-squared goodness of fit tests. The best-fitting model was then applied to the number of encounters at each survey point to give a species-specific estimate of the density of individuals together with their associated confidence intervals. Finally, the density of all birds (Total Density) at each survey point was calculated by summing individual species densities. We divided Total Density into groups representing species of greater interest for biodiversity conservation on the island, namely Endemic Density and IUCN-Listed Density (Table 1). Species richness (Total, Endemic, IUCN-Listed) at each survey point

Table 1

Species names, level of endemism and IUCN status of the 22 bird species surveyed on Príncipe Island, West Africa. IUCN Globally Threatened categories: VU, Vulnerable; NT, Near-Threatened; LC, Least Concern. In addition, three species of swift and the cattle egret are included below. However, they were all encountered either flying over sites or were seen at too great a distance from the survey points to enable them to be included in abundance calculations and further analyses.

Species		Level of endemism	IUCN threat level
Cattle egret ^{NA}	<i>Bubulcus ibis</i>	None	LC
African green pigeon ^{NP}	<i>Treron calva virescens</i>	Sub-species endemic to Príncipe	LC
Gulf of Guinea pigeon ^{NP,e}	<i>Columba malherbii</i>	Species endemic to Príncipe, São Tomé and Annobón	LC
Lemon dove ^{NP}	<i>Columba larvata principalis</i>	Sub-species endemic to Príncipe	LC
Laughing dove ^{NP}	<i>Streptopelia senegalensis</i>	None	LC
Grey parrot ^{NP}	<i>Psittacus erithacus</i>	None	LC
Jacobin cuckoo ^{NP}	<i>Clamator jacobinus</i>	None	LC
Emerald cuckoo ^{NP}	<i>Chrysococcyx cupreus insularum</i>	Subspecies endemic to Príncipe and São Tomé	LC
São Tomé spinetail ^{NA,e}	<i>Zoonavena thomensis</i>	Species endemic to Príncipe and São Tomé	LC
Palm swift ^{NA}	<i>Cypsiurus parvus</i>	None	LC
Little swift ^{NA}	<i>Apus affinis</i>	None	LC
Blue-breasted kingfisher ^{NP}	<i>Halcyon malimbica dryas</i>	Sub-species endemic to Príncipe	LC
Malachite kingfisher ^{NP}	<i>Alcedo cristata nais</i>	Sub-species endemic to Príncipe	LC
Príncipe thrush ^{P,e,i}	<i>Turdus xanthorhynchus</i>	Species endemic to Príncipe	CR
Dohrn's thrush-babbler ^{P,e}	<i>Horrorhinus dohrni</i>	Genus endemic to Príncipe	LC
Príncipe sunbird ^{P,e}	<i>Anabathmis hartlaubii</i>	Species endemic to Príncipe	LC
Olive sunbird ^P	<i>Cyanomitra olivacea</i>	None	LC
Príncipe white-eye ^{P,e,i}	<i>Zosterops ficedulinus</i>	Species endemic to Príncipe	VU
Príncipe speirops ^{P,e,i}	<i>Speirops leucophaeus</i>	Species endemic to Príncipe	NT
Príncipe drongo ^{P,e,i}	<i>Dicrurus modestus</i>	Species endemic to Príncipe	NT
Starling spp. ^P	<i>Lamprolornis</i> spp	–	–
Príncipe golden weaver ^{P,e}	<i>Ploceus princeps</i>	Species endemic to Príncipe	LC
Chestnut-breasted negrofinch ^P	<i>Nigrita bicolor</i>	None	LC
Common waxbill ^P	<i>Estrilda astrild</i>	None	LC
Bronze manikin ^P	<i>Lonchura cucullata</i>	None	LC
Príncipe seedeater ^{P,e}	<i>Serinus rufobrunneus rufobrunneus</i>	Species endemic to Príncipe and São Tomé with three subspecies	LC

ⁱSpecies included in IUCN-listed species group.

^eIncluded in Endemic species group.

^PPasserine, for the purposes of Distance analysis.

^{NP}Non-passerine for the purposes of Distance analysis.

Table 2
Sites, habitat types, number of survey locations for study sites across Príncipe Island, West Africa.

N	Site name	Habitat type (altitude band)	Number of survey points
1	Rio Porco	Primary (low)	21
2	Camp Tomé	Primary (low)	20
3	A Mesa	Primary (high)	11
4	Pico do Príncipe	Primary (high)	20
5	Boca do Inferno	Primary (mid)	13
6	O Que Pipi	Primary (mid)	20
7	Camp Joaquim	Secondary	10
8	Pico Papagaio	Secondary	12
9	Morro Estanduarte	Secondary	9
10	Bela Vista	Agriculture	10
11	Ponta do Sol	Agriculture	10
12	Ribeira Izé	Agriculture	11
13	Belo Monte	Agriculture	10

included all species recorded as part of the distance sampling procedure.

We calculated density, species richness, diversity and evenness to capture different aspects of diversity. For all species combined, endemic and IUCN-listed species, we calculated total density for each survey point, each habitat and for the three primary forest altitudinal bands. Measures of species diversity were generated using both Simpson and Shannon indices. Evenness was estimated as Pielou's J and ranged from zero to one, approaching one where individuals are distributed equally across species.

Data analysis

We wished to explore whether avian assemblage structure differed between primary forest, secondary forest and agricultural habitats. This was done using non-metric multidimensional scaling (NMDS) coupled with analysis of similarity (ANOSIM), based on Bray–Curtis distances. For all analyses we used \log_{10} transformed standardised densities per site. NMDS used 500 iterations and 250 runs of both real and randomised data to produce a final ordination of minimum stress consisting of two axes and was implemented in PC-ORD v.6 (McCune & Mefford 2011). ANOSIM was based on 999 permutations and was conducted using R release 2.13.2. To quantify whether particular species are characteristic of the three main habitat types, we conducted Indicator Value analysis (Dufrene & Legendre 1997) based on a random reallocation procedure from 4999 permutations of sites among habitats and was conducted in PC-ORD v.6 (McCune & Mefford 2011).

Table 3
Mean (standard error where given) for characteristics of the avian assemblage across three major habitats (primary forest, secondary forest, agricultural areas) and primary forest from three altitudinal bands on Príncipe Island, west Africa.

	Agriculture	Secondary	Primary	Primary (high)	Primary (mid)	Primary (low)	Overall
Simpson diversity	0.77 (0.01)	0.76 (0.01)	0.68 (0.01)	0.62 (0.03)	0.73 (0.02)	0.69 (0.02)	0.71 (0.01)
Shannon diversity	1.63 (0.05)	1.59 (0.05)	1.34 (0.04)	1.15 (0.08)	1.49 (0.05)	1.38 (0.06)	1.45 (0.03)
Pielou's evenness	0.88 (0.01)	0.90 (0.01)	0.88 (0.01)	0.89 (0.16)	0.88 (0.01)	0.87 (0.01)	0.88 (0.00)
Total species richness	6.97 (0.24)	6.07 (0.28)	4.72 (0.17)	3.81 (0.28)	5.33 (0.28)	4.93 (0.26)	5.43 (0.14)
IUCN-listed richness	0.74 (0.09)	0.68 (0.07)	0.54 (0.06)	0.58 (0.13)	0.61 (0.12)	0.46 (0.09)	0.61 (0.05)
Endemic richness	3.77 (0.14)	3.49 (0.17)	2.98 (0.10)	2.87 (0.18)	3.21 (0.19)	2.88 (0.13)	3.24 (0.08)
No. of survey points	31	41	105	31	33	41	177
Proportion of total abundance accounted for by IUCN-listed species	0.13	0.13	0.15	0.14	0.17	0.14	0.14
Proportion of total abundance accounted for by endemic species	0.71	0.72	0.76	0.84	0.75	0.71	0.74

Associations with environmental attributes

Although we used simple ecological categories (primary, secondary and agriculture) to describe the three main habitat types on Príncipe, we recognise that within them there is considerable heterogeneity. Therefore, as the vegetation structural characteristics are known to influence avian species composition (e.g. Abrahamczyk et al. 2008; Gardner et al. 2009), we assessed the habitat associations of the bird community by characterising aspects of vegetation structure at each survey point. Measurements taken were: the number of trees making up the canopy within a 15 m radius of the point (Canopy Count); canopy cover estimated by counting the number of squares marked on a mirror (held horizontally in front of the field worker) covered by leaves and branches (Canopy Cover); the maximum visible height of the canopy measured using a rangefinder (Canopy Height); the average number of stems in three 1 m radius circles, 1 m above ground level (Ground Cover); the number of fruiting or flowering trees located using binoculars (Fruit/Flower) and the abundance of epiphytes (Epiphytes) recorded on a scale of 0 (none) to 3 (dense).

The broader landscape context in which a survey point is found could play an equally important role in explaining avian diversity and community structure (Devictor & Jiguet 2000; Gardner et al. 2009; Heikkinen et al. 2004). It is therefore likely that the extent of different land covers, such as primary and secondary forest will affect bird community composition. To assess landscape context we quantified the proportion of a 500 m buffer surrounding each survey point that was covered by land cover types in a GIS. Land covers (Primary Forest, Secondary Forest, Shade Agriculture, including all forms of agriculture with shade canopy cover, Non-Shade Agriculture, including low intensity subsistence plots of maize and vegetables) were based on a digitised version of a recent vegetation map of the island use (Diniz & De Matos 2002). Finally, the altitude of each survey point was taken from satellite derived remotely sensed data using a Digital Elevation Model (see Dallimer & Melo 2010 for details).

We wished to determine which landscape context and vegetation structure measures were most strongly related to species richness and density. Therefore, for each response variable (Total density, Endemic Density, Total Richness, Endemic Richness), we carried out a multiple regression, accounting for the lack of independence between survey points visited as part of the same site, by including site as a random effect in a mixed modelling framework. We used a Poisson error structure for the species richness data. Two sets of explanatory variables (landscape context and vegetation structure) were modelled separately in order not to over-specify the mixed models. We tested the co-linearity of the explanatory variables and discarded any with a Variance Inflation Factor (VIF)

Table 4

Mean (standard error) values of vegetation structure and landscape context variables for survey points within three habitat types on Príncipe Island, West Africa.

Variable	Habitat			Overall
	Agriculture ^a	Primary	Secondary	
Local scale				
Canopy Number	4.4 (0.7)	8.0 (0.5)	11.0 (1.4)	8.1 (0.5)
Canopy Height (m)	17.5 (1.5)	25.1 (0.7)	24.8 (0.8)	23.7 (0.6)
Canopy Cover (scale 0–32)	13.3 (1.9)	19.6 (0.8)	18.5 (1.2)	18.2 (0.6)
Ground Cover	7.8 (2.0)	3.5 (0.3)	5.2 (0.7)	4.6 (0.4)
Number of fruit/flowering trees	5.6 (0.7)	0.8 (0.3)	0.8 (0.2)	1.6 (0.3)
Abundance of epiphytes (scale 0–3)	0.5 (0.1)	1.4 (0.1)	0.9 (0.1)	1.1 (0.1)
Landscape scale				
Altitude (m)	114 (9)	399 (19)	279 (16)	321 (14)
Proportion of primary forest in a 500 m buffer	0.00	0.93	0.33	0.63
Proportion of secondary forest in a 500 m buffer	0.00	0.00	0.24	0.06
Proportion of shade agriculture in a 500 m buffer	0.42	0.00	0.43	0.17
Proportion of non-shade agriculture in a 500 m buffer	0.55	0.07	0.00	0.14

^a Other land uses, such as human settlements and rivers, comprised 0.03 of the buffers surrounding survey points in the agricultural habitat.

that was greater than three (Zuur et al. 2010). For landscape context, the proportion cover by secondary forest and altitude exceeded this threshold, leaving a final set of three variables (proportion cover by primary forest, shade agriculture and non-shade agriculture). The VIF threshold was not exceeded by any variables in the vegetation structure set.

For each set of explanatory variables, we constructed all possible model combinations and used AICc comparisons to identify the most parsimonious model and also a subset of models offering parsimonious explanations for variations in the data. This subset includes those with an AICc score within 2 of the minimum (Burnham & Anderson 2002). We calculated the model averaged parameter estimates for this model set using model weights. Further, we examined the relative importance of each variable in explaining species richness by calculating w_i , the Akaike weight, for each predictor variable.

Results

From across 177 survey points, 2726 detections of 23 species (Table 1) were recorded. Of these detections, most (66.5%) were

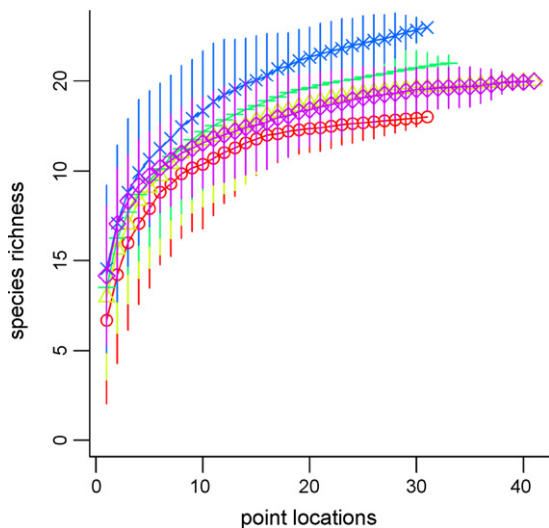


Fig. 2. Sample-based species accumulation curves for all species across habitats (blue – agriculture, green – secondary, yellow – primary (low altitude), purple – primary (mid-altitude), red – primary (high altitude)). Vertical lines show 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

endemic species and 9.3% were IUCN-listed. Four species accounted for over half (56%) of all detections (Dohrn’s thrush-babbler, grey parrot, Príncipe golden weaver and Príncipe sunbird). Many species were widespread; nine were found across all three habitats and eight occurred in at least 50% of the survey points. The most abundant species, Dohrn’s thrush-babbler, was present at 175 of the 177 points. The most widely occurring IUCN-listed species (Príncipe speirops) was found at 131 (74.0%) survey points in all habitats. The Príncipe drongo was substantially less common (10 survey points), but also occurred in all three habitats. In contrast the Príncipe thrush (11 points) and Príncipe white-eye (10 points) were found only in primary rainforest.

All richness and diversity indices were higher for survey points in secondary forest and agriculture habitats than in primary forest at all altitudes (Table 3). There was little difference between the species accumulation curves, with secondary forest and the three primary forest altitude bands flattening after 10–15 survey points. The curve for agricultural sites shows some evidence of a continuing increase, suggesting that further fieldwork would have uncovered more species (Fig. 2).

Endemic species accounted for a greater proportion of total avian abundance at high altitude primary forest survey points (Table 3). Two endemic species (Príncipe thrush and white-eye) occurred exclusively in primary rainforest; over 50% of thrush total abundance was within the high altitude band, while nearly

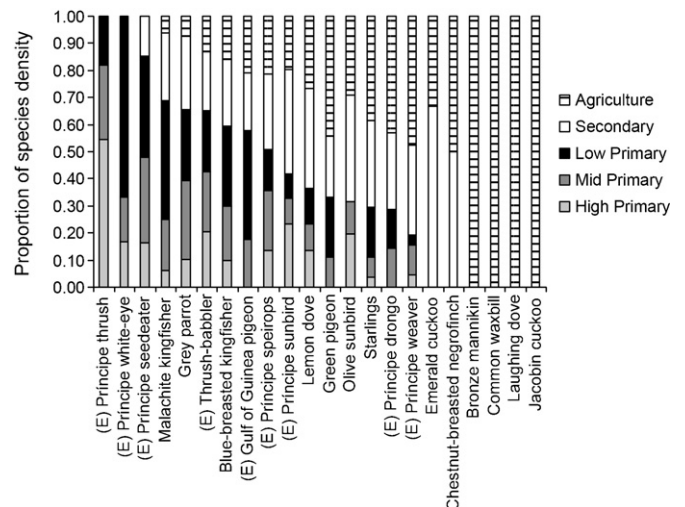


Fig. 3. The proportion of species total densities across all sites found in each of five habitat types, on Príncipe Island, West Africa. Endemic species are indicated (E).

Table 5
 Relationships between four measures of the avian assemblage (total density and richness, endemic density and richness) and (a) landscape context and (b) vegetation structure on Príncipe Island, West Africa. Akaike weights (wi) and model averaged parameter estimates (standard error) are given for variables that appeared in the $\Delta AIC < 2$ model set and those shown in bold in the best, most parsimonious, model. Where no parameter estimate is shown, it did not appear in the $\Delta AIC < 2$ model set. N indicates that the null model (i.e. the model that just contained the random effects of site) appeared in the $AIC < 2$ set. This suggests that a model that just includes the random effect of site offered an equally plausible explanation of the data. * indicates that the null model was the best, most parsimonious model and additional explanatory variables therefore did not improve the model fit. No parameter estimates are therefore presented and the intercept and explanatory power refer to the null model only.

Response	Intercept		Proportion primary		Proportion shade-agriculture		Proportion non-shade-agriculture		R^2
	β	wi	β	wi	β	wi	β	wi	
(a)									
Total density (birds/km ²)	5114.40 (771.0)		-1377.5 (661.7)	0.77	1701.7 (695.3)	0.77	-84.50 (1195.9)	0.45	0.304
Endemic density (birds/km ²)	26.11 (2.26)		-3.86 (2.70)	0.36	10.34 (3.32)	1	3.55 (3.06)	0.26	0.209
Total richness	1.92 (0.06)		-0.40 (0.08)	1	0.06 (0.12)	0.28	-	-	0.267
Endemic richness	1.34 (0.08)		-0.27 (0.10)	1	-	-	-0.11 (0.16)	0.31	0.128
Response	Intercept	Canopy Cover	Canopy Height (m)	Canopy Number	Epiphytes	Fruiting/flowering	Ground Cover		
	β	β	β	β	β	β	β	β	R^2
(b)									
Total density (birds/km ²)	4651.61 (620.30)	-	27.92 (17.57)	-28.85 (19.55)	0.48	-	-26.36 (21.45)	0.38	0.265
Endemic density (birds/km ²) ^N	3622.30 (418.83)	-	17.46 (14.43)	-28.45 (15.73)	0.78	0.08	-18.19 (31.6)	0.08	0.161
Total richness ^N	1.71 (0.09)	-	-	-	-	-	-	-	0.112
Endemic richness ^N	1.27 (0.11)	-0.008 (0.005)	-	0.003 (0.006)	0.13	-0.02 (0.05)	0.12	0.009 (0.01)	0.038

70% of Príncipe white-eye abundance was in low altitude primary forest. A further endemic species, the Príncipe seedeater, was restricted to primary and secondary forest. Four non-endemic species (Jacobin cuckoo, bronze mannikin, common waxbill and laughing dove) occurred exclusively in agricultural sites, and two further non-endemics (chestnut-breasted negrofinch and emerald cuckoo) were not found in primary forest (Fig. 3).

All habitats showed similar patterns of species dominance, and, in general, the same endemic species were dominant across habitats, with major differences in relative species abundances only occurring for infrequently encountered species (Fig. 4). Six species were recorded in only one habitat. In agricultural sites, these were non-endemic, widespread species, while for primary forest uncommon species were those that were both highly range-restricted endemics and IUCN-listed. The indicator species analysis mirrored these patterns. Two endemic species (Príncipe thrush – Indicator Value = 0.67, $p = 0.033$, Príncipe white-eye – Indicator Value = 0.67, $p = 0.031$) were identified for primary forest and a single non-endemic species (laughing dove – Indicator Value = 1.0, $p = 0.005$) for agricultural habitats. No species were indicators of secondary forest (Table 4).

Non-metric multidimensional scaling revealed differences in assemblage patterns between habitat types for both the total and endemic species assemblages (Fig. 5). Plots represented 95% and 91% of the community dissimilarity respectively. Within the total assemblage plot, there were significant differences in community structure between the habitat types (ANOSIM, $R = 0.39$, $p = 0.008$). Sites from the same habitat types are well clustered with secondary forest sites intermediate between primary and agricultural site clusters (Fig. 5a). There were also significant differences in community structure for the endemic species assemblage ($R = 0.50$, $p = 0.004$), however the NMDS plot reveals two main clusters, one containing the majority of the primary and secondary forest sites, and one containing agriculture sites together with a single secondary forest site (Fig. 5b).

Landscape context variables explained between 12.8% (endemic richness) and 30.4% (total density) of the variation in the four avian assemblage measures (Table 5a). There was a negative relationship between the proportion of primary forest surrounding a survey point and all four measures of the avian assemblage. In contrast, both total and endemic density were enhanced as the amount of shade agriculture in the landscape increased. Vegetation structure offered generally poor explanatory power (Table 5b). The null model (i.e. that which only contained site as a random effect) gave the most parsimonious explanation of variation in total richness. Although endemic richness did decrease with canopy cover, explanatory power was low (3.8%). The most important predictors of total and endemic density were a positive relationship with canopy height, a negative response to canopy number and ground cover. This suggests that density increases in forest characterised by a higher, more open structure.

Discussion

The future of tropical forest biodiversity will increasingly rely on the effective management of both agricultural and novel habitats (e.g. Gardner et al. 2009; Perfecto & Vandermeer 2008) not least given that forests continue to lose biodiversity (e.g. Bradshaw et al. 2009) and threats to their extent and integrity mount (e.g. Balmford et al. 2005; Field et al. 2008; Fitzherbert et al. 2008). Here we demonstrate that some endemic species can occur at high abundances in novel and agricultural habitats which therefore have the potential to be an important resource for their conservation. Survey points in the modified habitats were, on average, more diverse, with a greater total number of birds observed when compared to

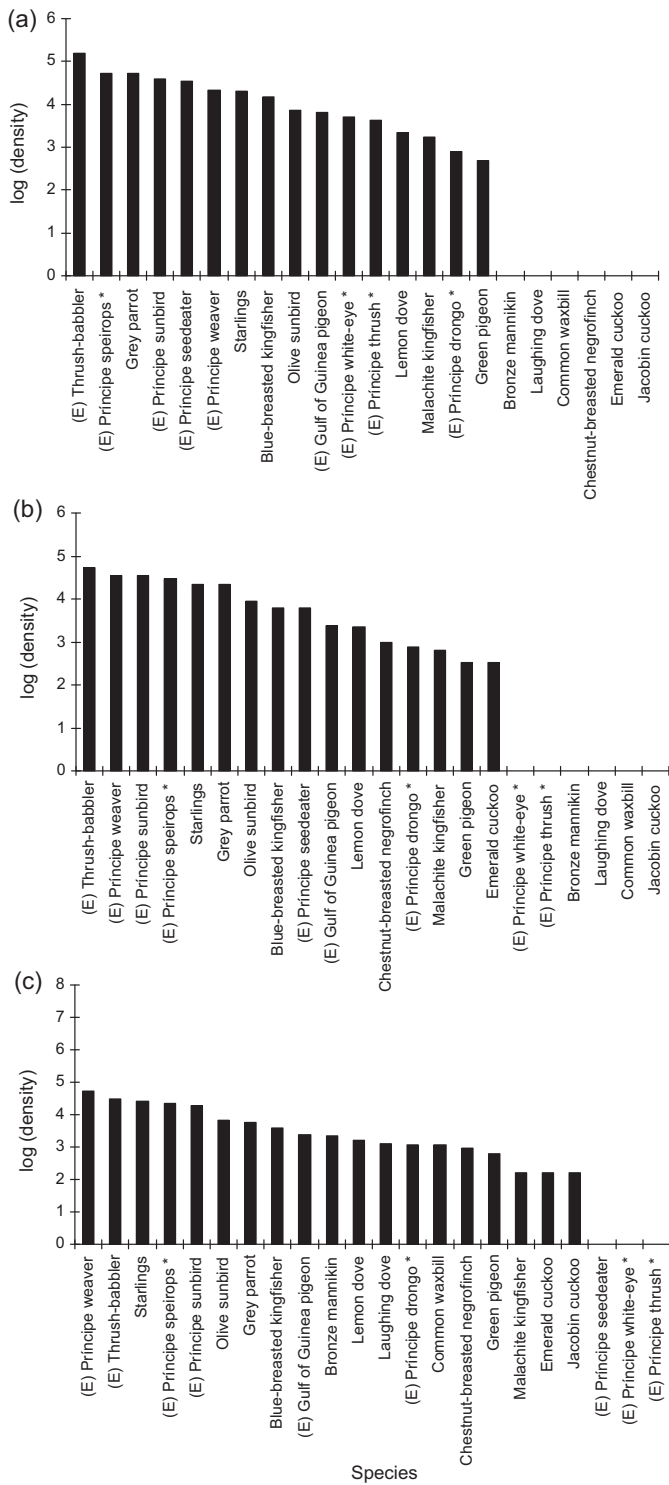


Fig. 4. Species ranked by their density for (a) primary forest, (b) secondary forest and (c) agricultural sites. Endemic species are indicated (E). *IUCN listed species.

primary forest – a pattern which held when considering the overall abundance of endemic species and IUCN-listed species. Indeed, the same, largely endemic, species dominated across the habitats. However, at the individual species level, abundances were higher in primary forest for seven of the nine endemics (Fig. 4). It is often the taxa that are of highest conservation priority, such as regional forest endemics, that are most at risk of extinction in altered habitats (Posa & Sodhi 2006; Scales & Marsden 2008). Although on Príncipe the number of endemic and IUCN-listed species

encountered at each survey point was broadly similar across all habitats (cf. Bhagwat et al. 2008), two notable species from a conservation point of view, the IUCN-listed Príncipe thrush and Príncipe white-eye, were found solely within primary forest.

Landscape effects are important determinants of biodiversity in human-modified tropical agro-ecosystems (e.g. Tschamtkke et al. 2008). This is likely to be especially true of birds, given their high mobility. On Príncipe, the amount of shade agriculture within a 500 m buffer of the survey point was associated with increased abundances of both the total avian community and endemic species only. The maintenance of structurally complex habitats in human-modified environments has been shown to enhance the persistence of forest specialist species (Lamb et al. 2005; Scales & Marsden 2008). Here, vegetation structure attributes were generally weak predictors of the density and richness of the avian assemblage. Nevertheless, variables which are indicative of forested landscapes, such as a high canopy and less ground cover vegetation were related to enhanced Total and Endemic density.

Endemic communities on oceanic islands are susceptible to human-driven habitat change (Diamond et al. 1989; Fordham & Brook 2010; Ricklefs & Bermingham 2002), and birds on islands are particularly vulnerable to extinction (Baillie et al. 2004; Johnson & Stattersfield 1990). The species occurrence data presented here, which are based on a single visit, do not provide any indication of the long-term viability of the endemic bird community in human modified habitats (Gardner et al. 2009). Nonetheless, with a handful of important exceptions, the endemic birds of Príncipe appear to have been able to adapt to the altered land uses that dominate much of the island and endemic species are the most dominant across all habitats. This result joins a body of work that runs contrary to the idea that high levels of extinctions on islands reflect an intrinsically lower adaptive potential of island species compared to their continental relatives (e.g. Whittaker and Fernández-Palacios 2007). In fact, endemic island forms are often examples of fast adaptation to the peculiar insular environments that have no parallel on the mainland (e.g. Melo et al. 2011; Millien 2006). At least in their native habitat, island endemics are often the most abundant species (e.g. Gillespie et al. 2008; Rosindell & Phillimore 2011). On Príncipe, this may be because the alterations in land use were not severe, as agriculture on the island has relied on shade forests and the maintenance of high altitude forest as a source of water. Equally, the pattern of endemic adaptation may be biased as the most drastic human interventions (replacing lowland forest with sugarcane plantations) occurred several hundred years ago. The surviving avian community may have therefore already been 'filtered' by undocumented human-mediated extinctions (Biber 2002). Nevertheless, on Príncipe two endemics are restricted to the primary forest and it is these species (Príncipe thrush, Príncipe white-eye), together with their forest habitat, that are of highest conservation concern.

Protected areas should always play the most prominent role in biodiversity conservation, as they are uniquely placed to be able to protect native, largely unmodified habitats and the scarce habitat specialists that these areas can contain. On Príncipe, the primary forest retains an avian community which is notably different from those found elsewhere on the island as it includes both all endemic and all IUCN-listed species. This native forest should therefore remain as the centrepiece of conservation efforts on the island. However, we also demonstrate that agricultural habitats can be valuable for biodiversity conservation, containing substantial numbers of endemic and globally threatened species, and should not be overlooked. A two-tier approach to biodiversity conservation is therefore required (cf. Jackson & Hobbs 2009). The conservation value of the primary rainforest on Príncipe is already known to be high (e.g. Fishpool & Evans 2001), and this forest needs to be retained in its current extent. Second, a good quality matrix, with

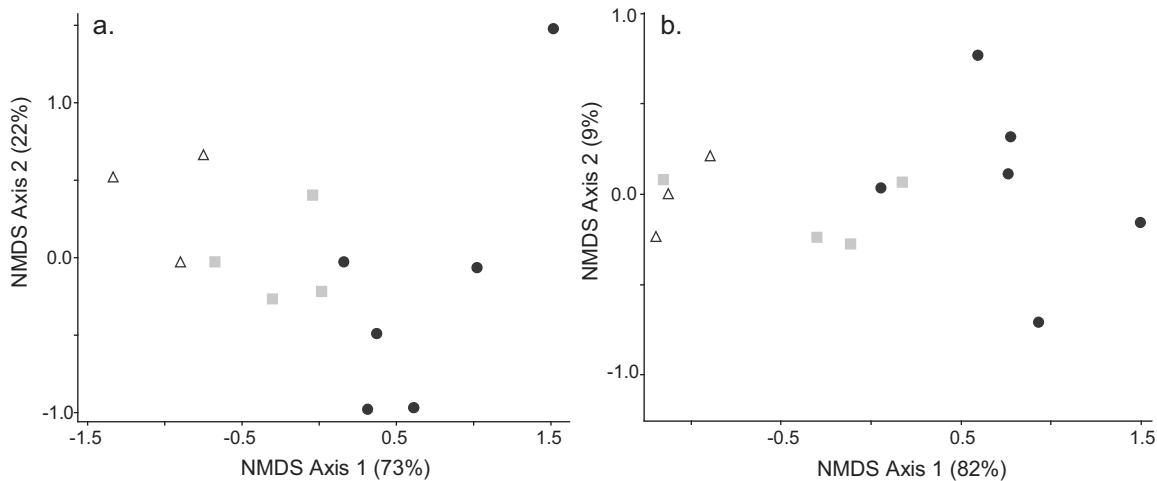


Fig. 5. Non-metric multidimensional scaling (NMDS) ordinations of bird community assemblage at each site. (a) All species. Stress=0.09. (b) Endemic species only. Stress=0.10. Circles = primary. Squares = secondary. Triangles = agriculture. Percentages on axis headers indicate the proportion of the dissimilarity in bird assemblage represented by that axis.

a complex vegetation structure, able to sustain the largest possible number of endemics needs to be maintained. This is particularly relevant on small islands, and such an approach is likely to have growing relevance as biodiversity losses continue. Human modified habitats will be increasingly required to provide some refuge for forest biodiversity in areas that have been subject to intense human impacts.

Acknowledgements

We thank Eng. Salvador Sousa Pontes, from the Department of Nature Conservation, for arranging permits. On Príncipe we are grateful to A and K Salvaterra; R Delpont and P Bosman of the Bom-Bom Island Resort and the Society for Conservation and Development. Bikegila and Sático were indispensable guides in the forests. N Collar and R Prys-Jones supported our grant applications. ZG Davies provided useful discussion and comments. The fieldwork was funded by the University of Edinburgh's Davis Expedition Fund, the British Ecological Society and the British Ornithologists' Union. MD holds an EU-FP7 Marie-Curie Fellowship.

References

Abrahamczyk, S., Kessler, M., Putra, D. D., Waltert, M., & Tschardtke, T. (2008). The value of differently managed cacao plantations for forest bird conservation in Sulawesi, Indonesia. *Bird Conservation International*, 18, 349–362.

Baillie, J. E. M., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2004). *2004 IUCN Red List of Threatened Species. A global species assessment*. Gland/Cambridge: IUCN.

Balmford, A., Green, R. E., & Scharlemann, J. P. W. (2005). Sparing land for nature: Exploring the potential impacts of changes in agricultural yield on the area needed for crop production. *Global Change Biology*, 11, 1594–1605.

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18, 182–188.

Bhagwat, S. A., Willis, K. J., Birks, H. J. B., & Whittaker, R. J. (2008). Agroforestry: A refuge for tropical biodiversity? *Trends in Ecology and Evolution*, 23, 261–267.

Biber, E. (2002). Patterns of endemic extinctions among island bird species. *Ecography*, 25, 661–676.

Bos, M. M., Steffan-Dewenter, I., & Tschardtke, T. (2007). The contribution of cacao agroforests to the conservation of lower canopy ant and beetle diversity in Indonesia. *Biodiversity and Conservation*, 16, 2429–2444.

Bradshaw, C. J. A., Sodhi, N. S., & Brook, B. W. (2009). Tropical turmoil: A biodiversity tragedy in progress. *Frontiers in Ecology and the Environment*, 7, 79–87.

Buchanan, G. M., Donald, P. F., Fishpool, L. D. C., Arinaitwe, J. A., Balman, M., & Mayaux, P. (2009). An assessment of land cover and threats in important bird areas in Africa. *Bird Conservation International*, 19, 1–13.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). New York, USA: Springer-Verlag.

Butler, S. J., Vickery, J. A., & Norris, K. (2007). Farmland biodiversity and the footprint of agriculture. *Science*, 315, 381–384.

Cincotta, R. P., Wisniewski, J., & Engelman, R. (2000). Human population in the biodiversity hotspots. *Nature*, 404, 990–992.

Dallimer, M., & King, T. (2008). Habitat preferences of the forest birds on the island of Príncipe, Gulf of Guinea. *African Journal of Ecology*, 46, 258–266.

Dallimer, M., King, T., & Atkinson, R. J. (2009). Pervasive threats within a protected area: Conserving the endemic birds of São Tomé, West Africa. *Animal Conservation*, 12, 209–219.

Dallimer, M., & Melo, M. (2010). Rapid decline of the endemic giant land snail *Archachatina bicarinata* on the island of Príncipe, Gulf of Guinea. *Oryx*, 44, 213–218.

Dallimer, M., Melo, M., Collar, N. J., & Jones, P. J. (2010). The Príncipe Thrush *Turdus xanthorhynchus*: A newly split, critically endangered, forest flagship species. *Bird Conservation International*, 20, 375–381.

Devictor, V., & Jiguet, F. (2000). Community richness and stability in agricultural landscapes: The importance of surrounding habitats. *Agriculture, Ecosystems and Environment*, 120, 179–184.

Diamond, J. M., Ashmole, N. P., & Purves, P. E. (1989). The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society London Series B*, 325, 469–477.

Diniz, A. C., & De Matos, G. C. (2002). Carta de Zonagem Agro-Ecológica e da Vegetação de S. Tomé e Príncipe: Ilha de S. Tomé. *Garcia de Orta, Ser Botanica*, 15, 1–22.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, 67, 345–366.

Field, C. B., Campbell, J. E., & Lobell, D. B. (2008). Biomass energy: The scale of the potential resource. *Trends in Ecology and Evolution*, 23, 53–112.

Fishpool, L. D. C., & Evans, M. I. (2001). *Important bird areas in Africa and associated islands: Priority sites for conservation*. Cambridge: BirdLife International.

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Bruhl, C. A., Donald, P. F., et al. (2008). How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution*, 23, 538–545.

Fordham, D. A., & Brook, B. W. (2010). Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation*, 19, 329–342.

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., et al. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, 12, 561–582.

Gillespie, R. G., Claridge, E. M., & Roderick, G. K. (2008). Biodiversity dynamics in isolated island communities: Interaction between natural and human-mediated processes. *Molecular Ecology*, 17, 45–57.

Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, 307, 550–555.

Heikkinen, R. K., Luoto, M., Virkkala, R., & Raino, K. (2004). Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology*, 41, 824–835.

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., et al. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, 15, 1–7.

IUCN. (2010). *2010 Red List of Threatened Species*. Geneva: IUCN.

Jackson, S. T., & Hobbs, R. J. (2009). Ecological restoration in the light of ecological history. *Science*, 325, 567–569.

Johnson, T. H., & Stattersfield, A. J. (1990). A global review of island endemic birds. *Ibis*, 132, 167–180.

Jones, P. J. (1994). Biodiversity in the Gulf of Guinea: An overview. *Biodiversity and Conservation*, 3, 772–784.

Jones, P. J., & Tye, A. (2006). *The birds of São Tomé and Príncipe, with Annobón: Islands of the Gulf of Guinea*. Oxford: British Ornithologists' Union.

Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science*, 310, 1628–1632.

- Mascaro, J., Becklund, K. K., Hughes, R. F., & Schnitzer, S. A. (2008). Limited native plant regeneration in novel, exotic-dominated forests on Hawai'i. *Forest Ecology and Management*, 256, 593–606.
- Mattison, E. H. A., & Norris, K. (2005). Bridging the gaps between agricultural policy, land-use and biodiversity. *Trends in Ecology and Evolution*, 20, 610–616.
- Marris, E. (2009). Ragamuffin earth. *Nature*, 460, 450–453.
- McCune, B., & Mefford, M. J. (2011). *PC-ORD. Multivariate analysis of ecological data. Version 6.0.*
- Melo, M., (2007). *Bird speciation in the Gulf of Guinea island system.* Unpublished PhD Thesis. University of Edinburgh.
- Melo, M., & Dallimer, M. (2009). Is there an undiscovered endemic scops owl *Otus* sp on Príncipe Island? *Malimbus*, 31, 109–115.
- Melo, M., Bowie, R. C. K., Voelker, G., Dallimer, M., Collar, N. J., & Jones, P. J. (2010). Multiple lines of evidence support the recognition of a very rare bird species – The Príncipe Thrush. *Journal of Zoology*, 282, 120–129.
- Melo, M., Warren, B. H., & Jones, P. J. (2011). Rapid parallel evolution of aberrant traits in the diversification of the Gulf of Guinea white-eyes (Aves, Zosteropidae). *Molecular Ecology*, 20, 4953–4967.
- Millien, V. (2006). Morphological evolution is accelerated among island mammals. *PLoS Biology*, 4, e321.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
- Peet, N. B., & Atkinson, P. W. (1994). The biodiversity and conservation of the birds of São Tomé and Príncipe. *Biodiversity and Conservation*, 3, 851–867.
- Perfecto, I., Mas, A., Dietsch, T., & Vandermeer, J. (2003). Conservation of biodiversity in coffee agroecosystems: A tri-taxa comparison in southern Mexico. *Biodiversity and Conservation*, 12, 1239–1252.
- Perfecto, I., & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems. *Annals of the New York Academy of Sciences*, 1134, 173–200.
- Posa, M. R. C., & Sodhi, N. S. (2006). Effects of anthropogenic land use on forest birds and butterflies in Subic Bay, Philippines. *Biological Conservation*, 129, 256–270.
- Ricklefs, R. E., & Bermingham, E. (2002). The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography*, 11, 353–361.
- Rosindell, J., & Phillimore, A. B. (2011). A unified model of island biogeography sheds light on the zone of radiation. *Ecology Letters*, 14, 552–560.
- Sadler, J. P. (1999). Biodiversity on oceanic islands: A palaeoecological assessment. *Journal of Biogeography*, 26, 75–87.
- Scales, B. R., & Marsden, S. J. (2008). Biodiversity in small-scale tropical agroforests: A review of species richness and abundance shifts and the factors influencing them. *Environmental Conservation*, 35, 160–172.
- Schroth, G., Fonesca, G. A. B., Harvey, C. A., Gascon, C., Vasconcelos, H. L., & Izac, A. M. N. (2004). *Agroforestry and biodiversity conservation in tropical landscapes.* Washington: Island Press.
- Schroth, G., & Harvey, C. A. (2007). Biodiversity conservation in cocoa production landscapes: An overview. *Biodiversity and Conservation*, 16, 2237–2244.
- Simons, T. R., Alldredge, M. W., Pollock, K. H., & Wettroth, J. M. (2007). Experimental analysis of the auditory detection process on avian point counts. *Auk*, 124, 986–999.
- Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M. M., Buchori, D., Erasmi, S., et al., 2007. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 4973–4978.
- Thomas, L., Buckland, A. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., et al. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5–14.
- Tscharntke, T., Sekercioglu, C. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P., & Tylianakis, J. M. (2008). Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, 89, 944–951.
- Vamosi, J. C., & Vamosi, S. M. (2008). Extinction risk escalates in the tropics. *PLoS One*, 3, e3886.
- Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island Biogeography: Ecology, Evolution, and Conservation.* Oxford: Oxford University Press.
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3–14.