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17

1 **Land-use intensification promotes exotic species in a tropical island bird**  
2 **assemblage**

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24

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19

## 1 **Abstract**

2 Habitat loss and exotic species are two key drivers of biodiversity loss. The importance of their  
3 interactions is widely recognized, but remains poorly understood. We used the endemic-rich bird  
4 assemblage of São Tomé Island to study this type of interactions. We built species-specific binomial  
5 generalized linear models for 33 terrestrial bird species, based on presence-absence data from 2398  
6 sampling points. Meta-analyses techniques revealed that land-use was more important in explaining  
7 distribution than topographic variables, rainfall or distance to coast for the studied bird species. Native  
8 species were more likely to occur in remote rainy forests at higher altitudes, while exotic species were  
9 more likely to occur in non-forested ecosystems, being associated to humanized lowland areas in the  
10 drier flat regions of São Tomé. The high invasibility of degraded forest ecosystems by exotic birds  
11 suggests that the high levels of disturbance favour these species. An analysis of species feeding guilds  
12 further suggests that these habitat associations might be linked to resource availability, since a large  
13 proportion of the exotics rely on seeds, which are clearly more available outside the best-preserved  
14 forests. Contrarily, very few native birds seem to be using this resource, and instead rely on more  
15 complex ecological interaction, such as carnivory and frugivory. Our results indicate that land-use  
16 intensification is the key driver of biodiversity changes on São Tomé, potentially by facilitating the  
17 expansion of exotics and demoting ecological complexity. Therefore, protecting the best-preserved  
18 forests is the single most important measure to ensure the conservation of native species.

## 19 **Keywords**

20 Anthropogenic land-use change; invasibility; ecological niches; forest threatened birds; species  
21 distribution model; introduced species; São Tomé

## 22 **1. Introduction**

23 Biodiversity is experiencing a fast global decline, marked by unusually high extinction rates  
24 (Pimm & Raven, 2000; IPBES, 2019). It is widely accepted that this decline is a consequence of  
25 human activities, and that habitat loss and exotic species are two of its key drivers (Vitousek et al.,

1 1997; Brooks et al., 2002; Gurevitch & Padilla, 2004; Maxwell et al., 2016). Exotic species are those  
2 that occur outside their native range due to human interference, either accidentally or intentionally.  
3 The independent role of each of these drivers has been extensively studied, but less is known about the  
4 interactions between them (Didham et al., 2007; Brook, Sodhi, & Bradshaw, 2008). Nevertheless, it  
5 has been shown that anthropogenic land-use change tends to facilitate the establishment and expansion  
6 of exotic species (Vitousek et al., 1997; Didham et al., 2005; Macdougall & Turkington, 2005). In  
7 fact, human activities often promote extensive changes to ecosystems, creating novel ecological niches  
8 that are occupied by exotic species (Didham et al., 2007).

9       The success of exotic species at colonizing new areas depends on a combination of their traits  
10 (invasiveness), and of the biotic and abiotic characteristics of the recipient ecosystem (invasibility)  
11 (Alpert, Bone, & Holzapfel, 2000; Enders, Hütt, & Jeschke, 2018). The exotic species often have  
12 broad ecological requirements, large geographic distributions, *r*-strategy selected traits and a long  
13 history of association with disturbed or anthropogenic habitats (human commensalism) (Mack et al.,  
14 2000; Sax & Brown, 2000). The ecosystems prone to the establishment of exotic species tend to be in  
15 historical geographic isolation, have low native species diversity, high levels of disturbance, and few  
16 competitors and predators (Alpert, Bone, & Holzapfel, 2000; Sax & Brown, 2000). Islands tend to  
17 have most of these characteristics and, therefore, their ecosystems are among the most susceptible to  
18 exotic colonization (Alpert, Bone, & Holzapfel, 2000; Sax & Brown, 2000) and exotic-induced  
19 extinctions (Simberloff, 1995; Blackburn et al., 2004).

20       Exotic species can have severe impacts on ecosystem processes and on native biodiversity  
21 (Vitousek et al., 1997; Simberloff et al., 2013). The catastrophic impacts on native biodiversity can be  
22 either through predation, herbivory, competition or habitat alteration (Mack et al., 2000; Blackburn et  
23 al., 2004). Nevertheless, it is difficult to identify and predict their effects (Gurevitch & Padilla, 2004).  
24 In Hawaii, for instance, different habitat requirements constrain competition between native and exotic  
25 birds, whose expansion is associated to land-use changes (Moulton & Pimm, 1983; Simberloff, 1995).

26       The importance of understanding the ecological interactions between exotic species and  
27 anthropogenic land-use change is recognized, but remains understudied (Didham et al., 2007). To  
28 understand the impacts of exotic species and propose efficient mitigation actions, it is vital to

1 distinguish if exotic species are causing the decline of native species, or simply taking advantage of  
2 anthropogenic land-use changes (Didham et al., 2005; Macdougall & Turkington, 2005). We used the  
3 endemic-rich bird assemblage of São Tomé Island to study the synergistic effects of land-use and  
4 exotic species on biodiversity as the relatively well-known land-use intensification gradient and the  
5 array of exotic birds on this island make it a good study system. Specifically, we (1) assess factors  
6 influencing bird species distribution, (2) contrast their effects on native and exotic species, with  
7 emphasis on the role of habitat degradation resulting from land-use intensification, and (3) explore  
8 how species traits relate to the observed habitat associations. Finally, we consider the implications of  
9 our findings for the conservation of native species worldwide.

## 10 **2. Materials and methods**

### 11 **2.1. Study area**

12 São Tomé is an 857 km<sup>2</sup> oceanic island in the Gulf of Guinea, Central Africa. Located just north  
13 of the Equator and 255 km west of continental Africa, it is part of the Democratic Republic of São  
14 Tomé and Príncipe. Despite the small size, its avifauna has a remarkable number of endemics (Jones  
15 & Tye, 2006; Le Saout et al., 2013). It is included in the “Guinean Forests of West Africa”  
16 biodiversity hotspot and its forests are part of a key biological ecoregion (Olson & Dinerstein, 1998;  
17 Myers et al., 2000). More recently, these forests were identified as the third most important for the  
18 conservation of forest birds worldwide (Buchanan, Donald, & Butchart, 2011).

19 As in many oceanic islands, human occupation in São Tomé led to the introduction, intentional or  
20 not, of many species from different taxonomic groups (Dutton, 1994; Jones & Tye, 2006; Figueiredo  
21 et al., 2011). Most exotic birds are small species, native to non-forested ecosystems in continental  
22 Africa, which did not have suitable habitat in São Tomé before human arrival, since the island was  
23 almost entirely covered by forest (Jones, Burlison, & Tye, 1991). The strong climatic gradients  
24 defined by the steep topography shaped the distribution of native vegetation types, as well as that of  
25 human colonization, which is usually accepted to have started during the late 15<sup>th</sup> century (Jones,  
26 Burlison, & Tye, 1991). Despite the recent human occupation of São Tomé, anthropogenic land-use

1 change was intense. The island remains dominated by forested ecosystems due to the difficult terrain.  
2 The inaccessible, rugged and wet areas in the southwest and centre of the island remain covered by  
3 native forest, surrounded by a rough belt of secondary forest resulting from logging and plantation  
4 abandonment. These forests are enclosed by extensive areas of shade plantations, a type of  
5 agroforestry focused on the production of export crops, such as coffee and cocoa. Interspersed among  
6 shade plantations are several non-forested areas, including oil palm monocultures, horticultures and  
7 open savannahs (Eyzaguirre, 1986).

## 8 **2.2. Bird sampling**

9 We gathered bird records using the BirdLife International São Tomé and Príncipe Initiative  
10 methodology (de Lima et al., 2017). São Tomé was divided in 1x1 km quadrats, clustered in groups of  
11 four to form 2x2 km quadrats (de Lima et al., 2017). A total of 31 2x2 km quadrats were excluded for  
12 having more than half of their area occupied by the ocean.

13 Each of the 2x2 km quadrats was sampled with five bird point counts in, at least, one of the four  
14 1x1 km quadrats. Point counts were separated by a minimum of 200 metres to ensure independence,  
15 and to guarantee that the environmental variability inside each quadrat was proportionally represented.  
16 A 10-minute count was carried out at each point, during which all bird species detected were recorded.  
17 Sampling took place between 6:00 am and 5:00 pm to maximize the number of sampled points.

18 We considered sampled all the 2x2 km quadrats that had five 10-minute point counts in one of the  
19 1x1 km quadrats. A total of 390 2x2 km quadrats, including most of those covered by forest, were  
20 sampled between 2009 and 2015 (de Lima, 2012; de Lima et al., 2017), and 91, including mostly those  
21 located in low-altitude plantations, were sampled between January and March 2017. Only five 2x2 km  
22 quadrats remained unsampled, mostly due to their inaccessibility.

## 23 **2.3. Characterizing environmental variables**

24 To model the distribution of São Tomé bird species, we obtained geographically explicit  
25 information on eight environmental variables (Appendix A). Six of these were continuous: altitude,  
26 ruggedness, slope, distance to coast, remoteness and rainfall. And the remaining two were categorical:

1 topography (flat areas, valleys, middle slope, upper slope, ridges) and land-use (native forest,  
2 secondary forest, shade plantation, non-forested areas). All variables were standardised to a common  
3 raster grid, using the nearest neighbour sampling method in Quantum GIS v. 2.8.3 and v. 2.14.8  
4 (Quantum GIS Development Team, 2009) and in Whitebox GAT (Lindsay, 2016). Topography was  
5 expressed in a 359x471 cell raster with 0.000833°x0.000833°-pixel size (i.e.,  $\approx 92$  metres), and was  
6 used as the reference raster in the “align rasters” tool (Quantum GIS Development Team, 2009).

## 7 **2.4. Data analysis**

8 We excluded aquatic species from the analysis, as well as those detected in less than 10 point  
9 counts ( $n = 18$ ). We also excluded points for which the land-use type identified by the field team was  
10 different from that on the land-use map ( $n = 5$ ), since this difference may result from land-use changes  
11 between land-use mapping and bird sampling. The bird species occurrence database used for the  
12 analysis had 33 bird species and 2398 sampled points (Appendix B).

13 All statistical analyses were made in R (R Development Core Team, 2017 - detailed description  
14 in Appendix C). Multicollinearity was tested for continuous variables using Spearman’s rank  
15 correlation coefficient, and ruggedness was excluded to maintain correlation coefficients below 0.8.  
16 Additionally, multicollinearity was tested between continuous and categorical variables using  
17 polyserial correlation, and between categorical variables using polychoric correlations. We checked  
18 for variance homogeneity and outliers using boxplots (Appendix B).

### 19 **2.4.1. Generalized linear models**

20 We randomly selected 70% of the point counts to be used as the training set to develop the  
21 binomial generalized linear models, while the remaining 30% were used to validate the models  
22 (Rushton, Ormerod, & Kerby, 2004). We used Variance Inflation Factors (VIF) to double-check  
23 multicollinearity among predictors, being careful to add categorical variables in one at a time to see  
24 their effect on VIF values. In line with the results of the correlation analysis, a VIF larger than 10  
25 supported the removal of the variable ruggedness from the analysis. For each species, we generated all  
26 possible models by recombining explanatory variables, and ranked them based on the Akaike



1 Information Criterion corrected for small sample sizes. Goodness of fit was analysed using  
2 McFadden's index. To examine model performance, we validated the predicted values and calculated  
3 the area under the receiving operating characteristic curve.

4 To identify which variables were most important to explain the presence of each species, we  
5 calculated the values of general dominance weight for each predictor and used 1000 permutations  
6 bootstrap analysis to measure accuracy (Azen & Traxel, 2009). Bird species were classified as native  
7 or exotic, and in four feeding guilds: carnivore (including insectivore), frugivore, granivore and  
8 omnivore (Jones & Tye, 2006; HBW Alive, 2017; Appendix B). To analyse the effect of each  
9 explanatory variable on the presence of each species, we performed a "Generic Inverse Variance"  
10 meta-analysis using the general dominance weights of each predictor as the value of effect size and its  
11 corresponding standard error. Each bird species was considered as an individual point in the meta-  
12 analysis, with a weight proportional to the inverse of the variance of the effect estimate. A random-  
13 effects meta-analysis using a DerSimonian and Laird approach was used to calculate mean effect sizes  
14 and 95% confidence intervals (Borenstein et al., 2009).

15 We explored the response of each species to environmental variables and linked them to origin  
16 (native, exotic) and feeding guilds using non-metric multidimensional scaling (NMDS - Minchin,  
17 1987). The NMDS plot was constructed based on Jaccard's index, using the presence-absence site-  
18 species matrix. The environmental variables were superimposed as vectors on the ordination diagram.  
19 We used the Spearman's rank correlation coefficient to evaluate the correlation between the two main  
20 ordination axes and each environmental variable, while the significance of the fitted vectors was  
21 assessed using 9999 permutations. To test for differences in the composition among bird species  
22 groups, we computed a PERMANOVA, which allows partitioning distance matrices among sources of  
23 variation. To describe the strength and significance of categorical variables to determine the variation  
24 of distances we used a permutation test with pseudo-F ratios (permutation = 9999; Anderson, 2001).

#### 25 **2.4.2. Mapping bird species richness and proportion**

26 To create a presence-absence map for each bird species, we identified an optimal cut-off value  
27 that ensured the best model performance for each species. The performance analysis implied the

1 validation of predicted values to calculate sensitivity, specificity, kappa and the associated standard  
2 deviation from a confusion matrix. The presence-absence maps for each species were used to compose  
3 estimated distribution maps for exotic species richness, proportion of native species and threatened  
4 species richness.

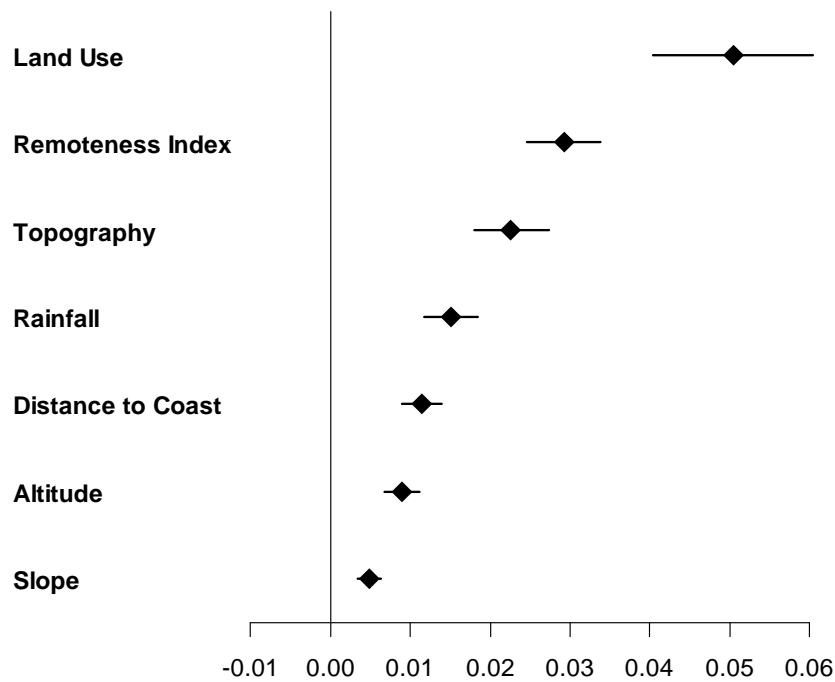
### 5 **3. Results**

6 On average, each of the 33 bird species appeared in 25.1% of the 2398 point counts, ranging from  
7 2120 (88.4%) for the São Tomé sunbird *Anabathmis newtonii* to 14 (0.6%) for the São Tomé grosbeak  
8 *Neospiza concolor* (Appendix B).

#### 9 **3.1. Determinants of bird species distribution**

10 There was considerable variation in the ability of models to accurately describe the occurrence of  
11 species (mean AUC =  $0.791 \pm 0.022$ ), ranging from 0.979 for the exotic golden-backed bishop  
12 *Euplectes aureus* to 0.595 for the native emerald cuckoo *Chrysococcyx cupreus* (Appendix D). The  
13 model performance of the exotic species (AUC =  $0.940 \pm 0.012$ ) was greater than that of the native  
14 species (AUC =  $0.736 \pm 0.021$ ).

15 The meta-analyses showed that land-use was the most important variable to predict the  
16 occurrence of bird species, followed by remoteness, topography and rainfall (Fig. 1 and Appendix D).  
17 Distance to coast and altitude had intermediate importance, while slope was the least important  
18 variable.

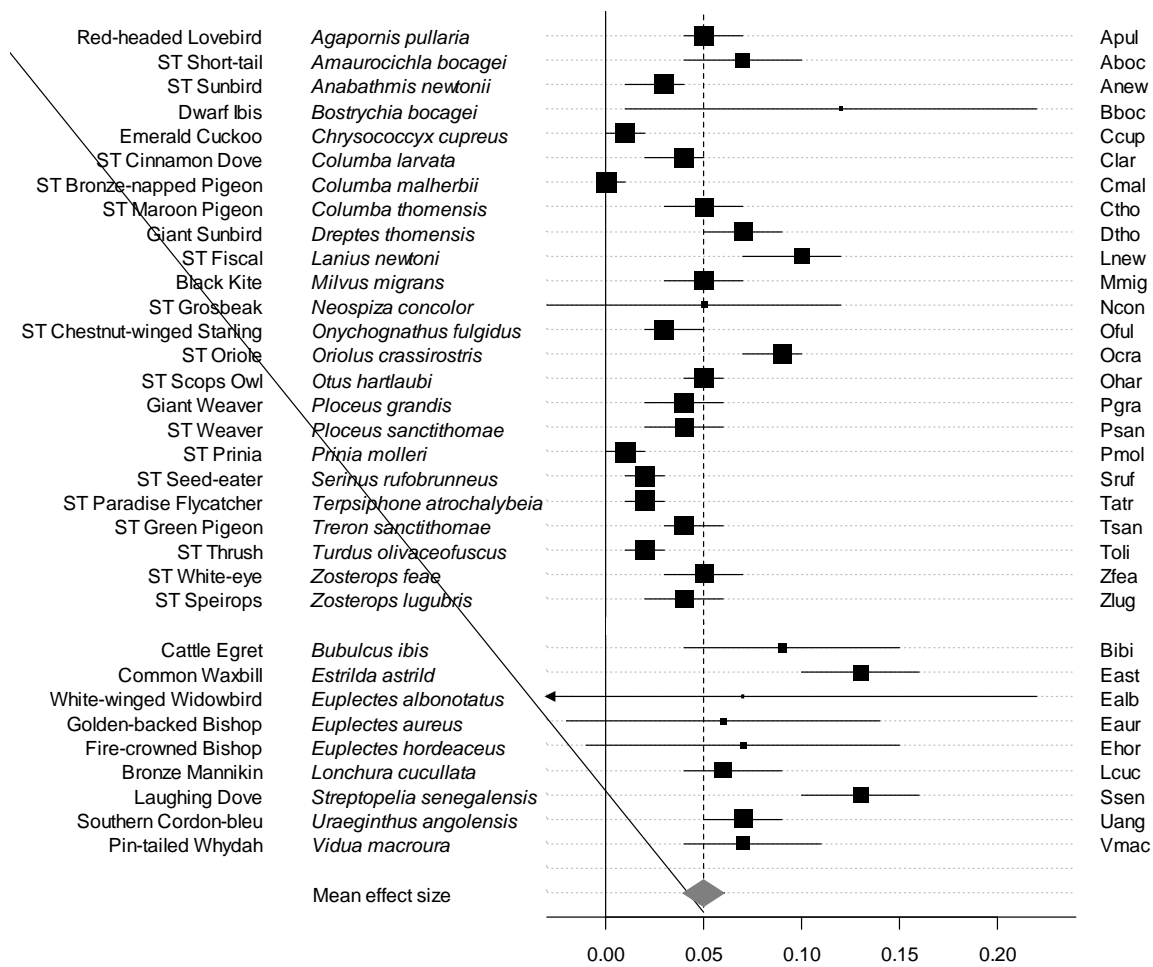


1 **Figure 1.**

2

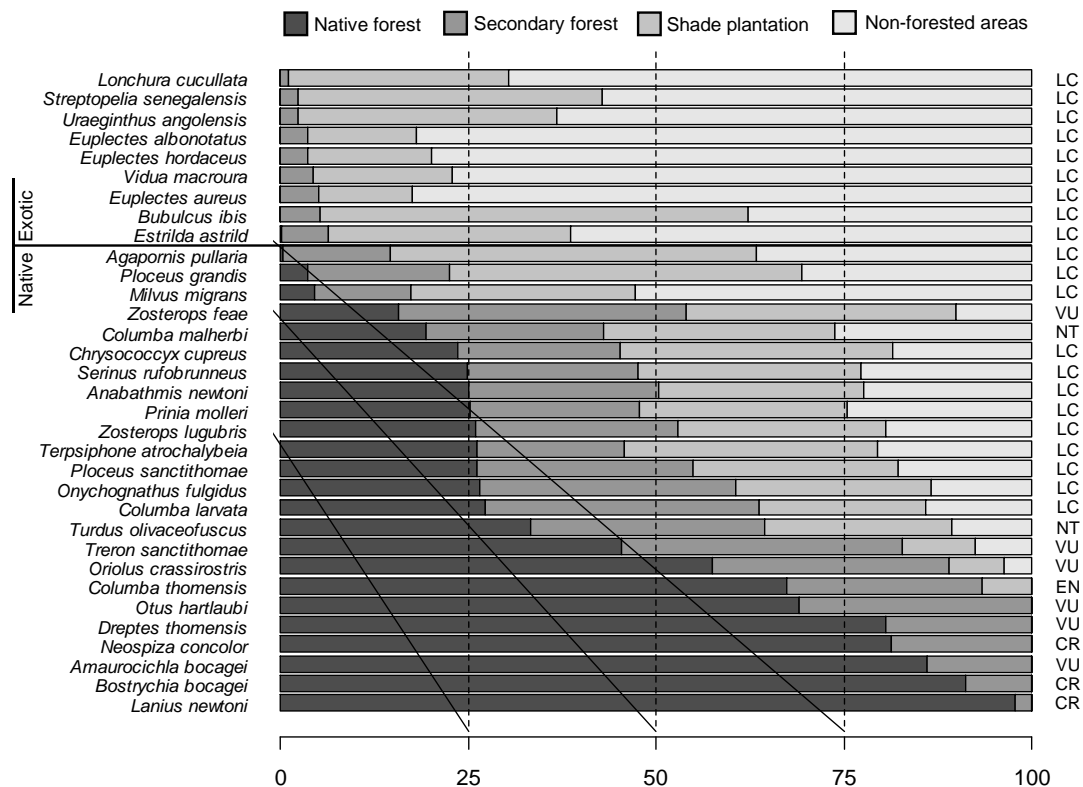
3 Land-use was the most important variable for most native species (15/24), while rainfall was the  
 4 most important for most of the exotics (7/9). Nevertheless, land-use was still very important to all nine  
 5 exotic species (Fig. 2), and especially for the common waxbill *Estrilda astrild* and the laughing dove  
 6 *Streptopelia senegalensis*. It was also important to native species restricted to forest (Fig. 2 and 3),  
 7 such as the dwarf ibis *Bostrychia bocagei*, the São Tomé fiscal *Lanius newtoni* and the São Tomé  
 8 short-tail *Amaurocichla bocagei*.

9



1 **Figure 2.**

2



1 **Figure 3.**

2

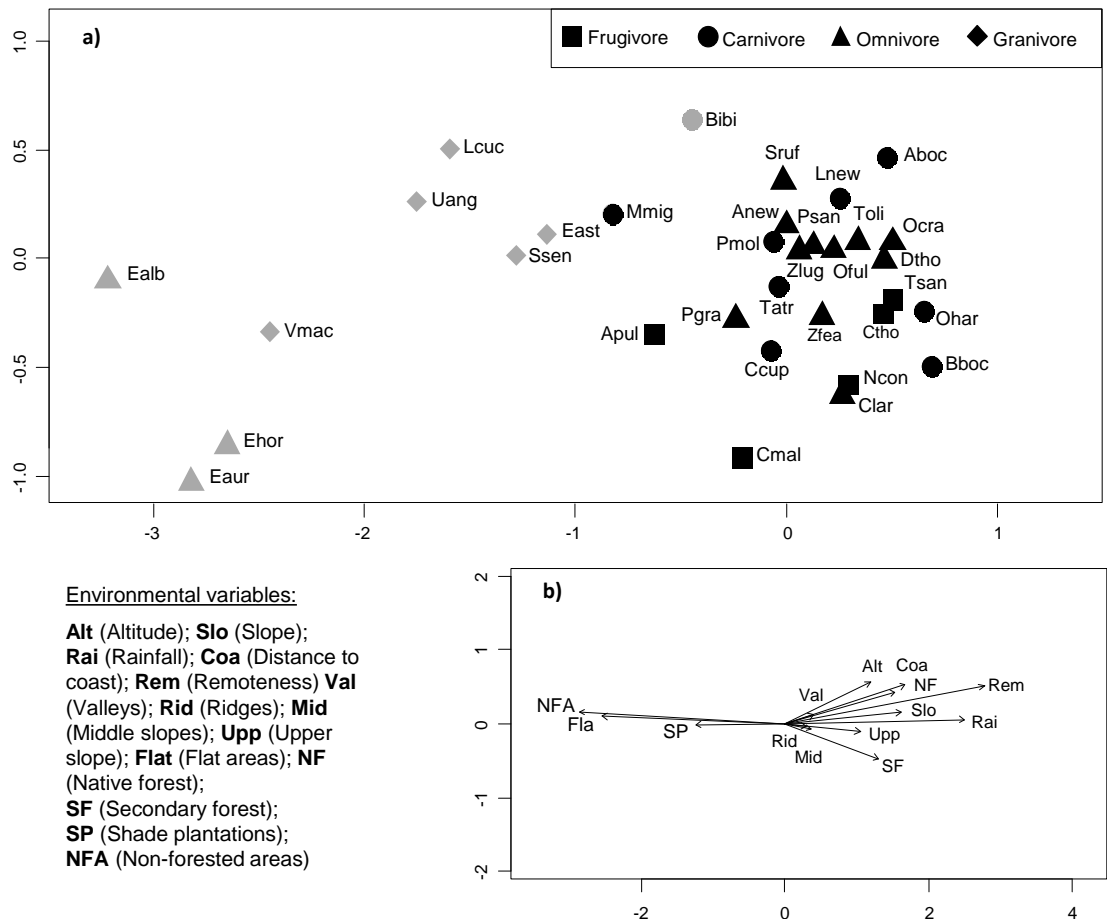
3 The overall pattern of habitat selection by native and exotic species was very different (Fig. 3).

4 All 24 native species occurred in forested land-use types. The dwarf ibis, the São Tomé fiscal and the  
 5 São Tomé short-tail were clearly associated to native forest, while other native species, like the green  
 6 pigeon *Treron sanctithomae* and the São Tomé white-eye *Zosterops feae*, were frequently found in  
 7 secondary forests. A few native species, such as the São Tomé seed-eater *Serinus rufobrunneus*, the  
 8 São Tomé prinia *Prinia mollerii* and the São Tomé sunbird, used all land-use types evenly. Only three  
 9 native species were found mostly in non-forested habitats: the resident black kite *Milvus migrans*; the  
 10 giant weaver *Ploceus grandis*, an endemic omnivore often found in plantations; and the red-headed  
 11 lovebird *Agapornis pullarius*, a common frugivore in plantations and open areas.

12 Contrasting with the native birds, all exotic species mostly occurred in non-forest land-use types  
 13 (Fig. 3). Eight out of nine had more than half of their presences in non-forested ecosystems, and only  
 14 one species, the common waxbill, occurred in native forest. The three omnivore *Euplectes* and the  
 15 granivore pin-tailed whydah *Vidua macroura* had more than 75% of presences in non-forested areas.

1 **3.2. Bird species response to environmental variables**

2 The NMDS (Fig. 4; no convergent solutions found, two dimensions, stress = 0.252), indicated  
 3 that all environmental variables were useful to explain the gradient of forest degradation represented  
 4 by the first axis ( $p < 0.05$ ; Appendix E).



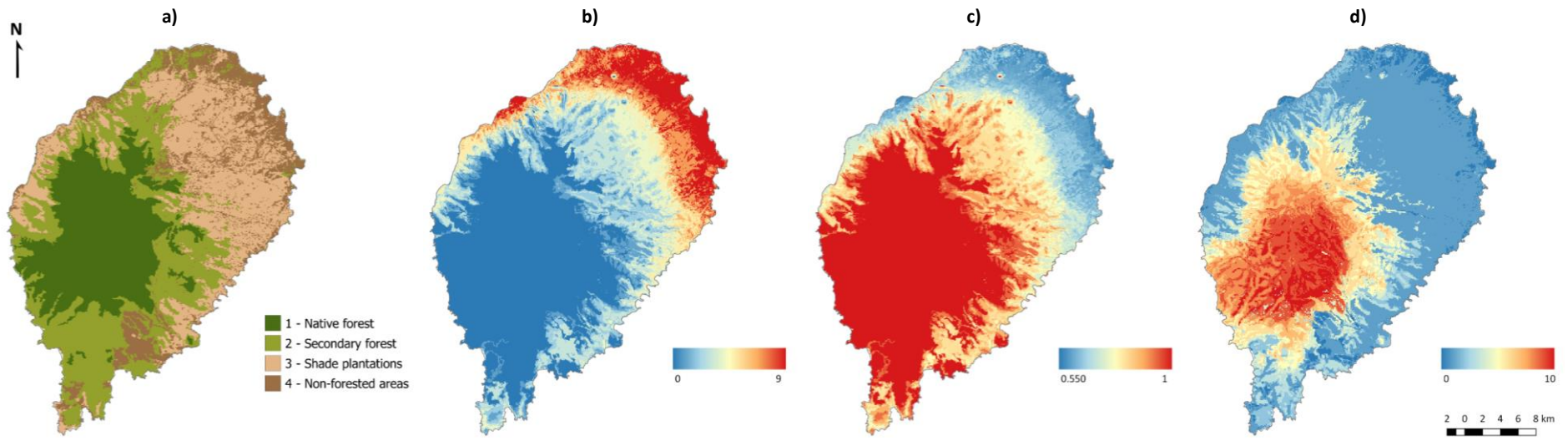
5 **Figure 4.**

6  
 7 The native and exotic species formed distinct groups (Fig. 4; PERMANOVA:  $R^2 = 0.13$ , pseudo-  
 8  $F_{1,32} = 4.46$ ,  $p < 0.001$ ), corroborating the abovementioned habitat associations identified on section  
 9 3.1. The native species tended to occur in remote areas with higher altitudes and rainfall, steeper  
 10 slopes, and away from the coast, while the exotics occurred in shade plantations and non-forested  
 11 areas, as well as in drier regions in accessible lowlands near the coast.

1           The feeding guilds also showed distinct patterns on the NMDS space (Fig. 4; PERMANOVA:  $R^2$   
2 = 0.152, pseudo- $F_{3,32} = 1.736$ ,  $p = 0.003$ ). The carnivores occurred in remote, rainy and steep forest  
3 areas, except for the black kite. All granivores are exotic and occurred in accessible lowlands  
4 dominated by shade plantations and non-forested areas. All frugivores are native, and omnivores  
5 include native and exotic species, but none of these feeding guilds showed clear associations with the  
6 environmental variables. The three omnivore *Euplectes* and the granivore pin-tailed whydah differed  
7 from the other species, being found mostly in non-forested areas, in the driest and most accessible  
8 lowlands (Fig. 4).

### 9 **3.3. Exploring distribution patterns**

10           The exotic species richness was higher in the driest, most intensive land-use types, such as non-  
11 forested areas and shade plantations, near the coast, and in the northeast of São Tomé, declining  
12 towards forested land-use types, down to no species in the native forest (Fig. 5a, b and Appendix F).  
13 On the other hand, the proportion of native species was highest in native and secondary forests, and  
14 there were no areas without native species (Fig. 5a and c). Threatened species were strongly associated  
15 with native forests (Fig. 5a and d).



1 Figure 5.



## 1 **4. Discussion**

2 Out of a selection of variables describing topography, climate, habitat and proximity to coast,  
3 land-use type was the most important factor determining the distribution of birds in São Tomé. Land-  
4 use type was particularly relevant to exotic species and to native species with a restricted distribution  
5 in the island. The native species occurred throughout the island, but preferred forested land-uses, while  
6 the exotics were strongly associated with low lying, flat, coastal areas with anthropogenic habitats.

### 7 **4.1. Anthropogenic ecosystems promote the spread of exotic species**

8 Land-use was the most important factor determining the distribution of birds in São Tomé, as it  
9 had already suggested (Jones & Tye, 2006; de Lima et al., 2013). This is in line with many other  
10 studies that have identified habitat as the primary determinant of species distribution at multiple spatial  
11 scales (Mazerolle & Villard, 1999; Tejeda-Cruz & Sutherland, 2004; Rocha, Virtanen, & Cabeza,  
12 2015). The importance of land-use type was followed by that of remoteness, rainfall and topography,  
13 all of which are interlinked: topography influences climate, and together they determine human  
14 occupation, and subsequently land-use (Jones, Burlison, & Tye, 1991). Nowadays, most intensive  
15 land-uses are closer to the coast, usually next to areas of higher human population density, clearly  
16 escaping higher altitudes, and the rugged and very wet centre and southwest of the island (Jones,  
17 Burlison, & Tye, 1991).

18 Rainfall was also markedly important to explain bird species distribution, especially to exotic  
19 species. In São Tomé, the occurrence of exotic species is strongly reliant on anthropogenic land-use  
20 types, and especially those located in the driest parts of the island, in the northeast (Jones, Burlison, &  
21 Tye, 1991). This preference seems to be linked to food availability, since most exotic species are  
22 heavily dependent on seeds, which are less available in forested and in wet areas due to the relative  
23 scarcity of gramineous plants (Diniz et al. 2002).

24 Our results also showed that land-use was very important to explain the distribution of five  
25 threatened endemics clearly associated to the best-preserved forest: the critically endangered dwarf

1 ibis and São Tomé fiscal, and the vulnerable São Tomé short-tail, giant sunbird *Dreptes thomensis* and  
2 São Tomé oriole *Oriolus crassirostris*.

3 Land-use had a lower importance for the remaining natives, including the most frequent  
4 endemics, which are habitat generalists and have a broad distribution throughout the island.

5 The land-use categories we used combined multiple vegetation types, meaning that there was  
6 considerable variation within each category. Since it is known that bird species are not evenly spread  
7 within land-use types (de Lima et al., 2017), variation within land-use types may be partially  
8 responsible for the overall low AUC values. The overall higher AUC for the distribution models of  
9 exotic species, and natives with restricted distribution in the island, are explained by clearer  
10 associations with the explanatory variables at the scale that they were measure, since these tended to  
11 have smaller sample sizes (Lobo, Jiménez-Valverde, & Real, 2008). Future studies should focus on  
12 understanding species distribution within land-use types, to assess subtle habitat variations at finer  
13 scales.

#### 14 **4.2. Land-use intensification decreases ecological complexity: insights from feeding guilds**

15 Until the late 15<sup>th</sup> century, São Tomé was almost entirely covered by forest (Jones, Burlison, &  
16 Tye, 1991). It is therefore not surprising that the native species occur mostly in forests and are adapted  
17 to explore forest food resources, such as fruits, insects and other animals. This adaptation helps  
18 explaining why they do not cope well with forest degradation, and it is known that primarily frugivore  
19 and insectivore species are particularly sensitive to deforestation (Naidoo, 2004; Sodhi & Smith, 2007;  
20 Newbold et al., 2013). On the other hand, most of São Tomé exotic birds occur in humanized areas  
21 and are either granivores or omnivores that are heavily reliant on seeds. These feeding guilds are  
22 easier to keep in captivity, increasing the chances of being introduced. Moreover, they are also better  
23 adapted to establish in disturbed areas, where seeds abound and where most native species are less  
24 well adapted (Enders, Hütt, & Jeschke, 2018; Cardador & Blackburn, 2019). This mismatch of  
25 ecological niches certainly reduces the competition between exotic and native bird species, facilitating  
26 the establishment of exotic species in disturbed environments (Alpert, Bone, & Holzapfel, 2000; Sax  
27 & Brown, 2000).

1 Similar distribution patterns of feeding guilds along forest degradation gradients have been  
2 described for other island (e.g. Hawaiian Islands: Moulton & Pimm, 1983) and non-island study  
3 systems (e.g.: Naidoo, 2004; Tejeda-Cruz & Sutherland, 2004; Waltert et al., 2005), suggesting that  
4 there is an underlying process.

5 Forests are widely considered stable and biodiverse ecosystems that hold complex ecological  
6 networks. It is therefore not surprising that forest loss and degradation lead to a simplification of  
7 ecological interactions. This is evident by the change in predominant feeding guilds: the demise of  
8 carnivores reflects a reduction in the number of trophic levels, while the reduction in frugivores and  
9 the increase of granivores suggests a replacement of mutualistic by exploitative animal-plant  
10 interactions (Sodhi & Smith, 2007).

#### 11 **4.3. Protecting São Tomé's unique biodiversity**

12 The land-use intensification gradient creates strong compositional changes: from forests  
13 assemblages that are entirely composed by native species to open environments that are rich in exotics  
14 (Atkinson, Peet, & Alexander, 1991; Hughes, Daily, & Ehrlich, 2002; Naidoo, 2004; Waltert et al.,  
15 2005; de Lima et al., 2013). However, many native species cope well with moderate levels of forest  
16 degradation, such as the São Tomé white-eye and the bronze-naped pigeon *Columba larvata* that are  
17 more frequent in secondary than in native forests. A few natives can even tolerate severe forest loss,  
18 such as the giant weaver and the black kite. The secondary forests seem to be acting as a transition  
19 zone, playing a key role in the protection of native forest species assemblage (Atkinson, Peet, &  
20 Alexander, 1991; Jones, Burlison, & Tye, 1991). Our results also highlight the importance of shade  
21 plantations for some native species, and while this system clearly holds less biodiversity value than  
22 either native or secondary forests, it can be managed to promote biodiversity and to help maintain the  
23 heavily forested São Tomé landscape (de Lima et al., 2014).

24 The dwarf ibis, the São Tomé grosbeak and the São Tomé fiscal are the bird species at greater  
25 risk of extinction, all of which being Critically Endangered endemics that are heavily reliant on native  
26 forest (de Lima et al., 2017; IUCN, 2018). The remaining threatened species are all endemics strongly  
27 associated with the native forest (IUCN, 2018), suggesting that the effective conservation of this forest

1 is the best single measure to ensure the persistence of São Tomé unique avifauna (de Lima, 2012).  
2 This is certainly true for most if not all forest bird assemblages, and there are already some successful  
3 examples of conservation where ecotourism acted as an economic incentive to reduce land-use  
4 intensification, namely by reducing deforestation and forest degradation, and by implementing  
5 biodiversity-friendly agricultural practices (Brandt & Buckley, 2018).

6 Besides land-use intensification, overexploitation and non-avian exotic species also seem to be  
7 significant threats to the persistence of São Tomé native birds. The precise impact of these threats is  
8 difficult to assess, since they often act synergistically with land-use intensification. Larger species,  
9 such as most native pigeons and the dwarf ibis, might favour forest land-use types not only for the  
10 habitat itself, but also for the reduced hunting pressure (Sodhi & Smith, 2007; Carvalho et al., 2015;  
11 de Lima et al., 2017). Exotic bird species do not seem to have a direct negative impact on the avifauna  
12 of São Tomé. However, a multitude of non-avian species have been introduced in São Tomé, notably  
13 mammals (Dutton, 1994) and plants (Figueiredo et al., 2011), and even though their impacts have not  
14 been studied, they are likely to be strongly negative (Blackburn et al., 2004).

#### 15 **4.4. Wider conservation implications**

16 Our results indicate that anthropogenic land-use change can promote the expansion of exotic  
17 species, corroborating the hypothesis that exotic dominance is an indirect consequence of  
18 anthropogenic ecosystem modifications, and that these are the key driver of native species loss  
19 (Vitousek et al., 1997; Didham et al., 2005, 2007; Macdougall & Turkington, 2005; Brook, Sodhi, &  
20 Bradshaw, 2008).

21 The decrease of restricted-range species in more intensive land-uses promoted the loss of  
22 distinctiveness, contributing to the ongoing global process of biotic homogenization (Olden &  
23 Rooney, 2006). Locally, this effect might be masked by the increase of species richness driven by  
24 exotic species, highlighting the need to acknowledge species origins and other traits to assess changes  
25 in biodiversity (de Lima et al., 2013). Furthermore, exotic species may contribute to biotic  
26 homogenization indirectly, through negative interactions with native species, which are known to be  
27 disproportionately high on island ecosystems (Clavero et al., 2009).

1 Our findings strongly match the distribution patterns predicted by taxon cycling, in which newly  
2 arrived species, typically pre-adapted to disturbed environments, occupy marginal coastal ecosystems  
3 (Sax & Brown, 2000; Jónsson et al., 2014). Therefore, it is expected that these introductions cause the  
4 extinction of species that are associated to the complex ecosystems occurring at the centre of the  
5 island. Recent research has shown that this might be a long-term consequence of introductions, since  
6 there can be a substantial delay between habitat loss and extinction (Jackson & Sax, 2010; Triantis et  
7 al., 2010). This extinction debt is difficult to assess, but can lead to underestimates of extinction rates  
8 and should thus be considered in conservation planning (Kuussaari et al., 2009).

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- 20

## 1 Captions for figures

2 **Figure 1.** Mean effect size of each environmental variable as determinant of bird distribution (n = 33  
3 species). The zero means no effect and horizontal bars indicate 95% confidence intervals. Land-use  
4 was the most important variable to explain the occurrence of bird species.

5

6 **Figure 2.** Forest plot with effect sizes for the importance of land-use to explain the occurrence of the  
7 33 studied bird species. The first 24 rows show native species and the following nine the exotic. Grey  
8 diamond indicates the mean effect size of land-use to all bird species combined. ESs were estimated  
9 using the general dominance weights and are represented by black squares, for which the area is  
10 proportional to weight (1/variance). The horizontal bars represent the 95% confidence intervals. The  
11 zero means no effect. In species common names ST stands for São Tomé.

12

13 **Figure 3.** Proportion of occurrence of each species by land-use type. Species are ranked according to  
14 land-use type preferences (native forest, secondary forest, shade plantation, and non-forested areas).  
15 Horizontal line separates native and exotic species, which show very distinct habitat preferences.  
16 Conservation status are represented next to the plot (CR – critically endangered; EN – endangered;  
17 VU – vulnerable; NT – near threatened; LC – least concern).

18

19 **Figure 4.** (a) Non-metric multidimensional scaling (NMDS) showing the relationship between origin,  
20 feeding guilds and environmental variables. Each symbol represents a species, identified by an  
21 abbreviation (see Fig. 2). The native species are shown in black and formed a group significantly  
22 distinct from that of the exotic species in grey. The shape of the symbol represents the feeding guild.  
23 (b) Relationship between environmental variables and the NMDS axes.

24

25 **Figure 5.** Maps showing the distribution of (a) land-use, (b) exotic species richness, (c) proportion of

1 native species and (d) threatened species richness. There was a clear opposite pattern in the  
2 distribution of exotic species richness and native species proportion. It is evident that exotic species  
3 thrive particularly well in land-use types most influenced by man (b). As a result, the assemblages of  
4 these land-uses are composed of up to one half of exotic species, whereas those of better-preserved  
5 habitats remain totally dominated by native species (c). Moreover, there is a strong association  
6 between the distribution of threatened species and that of native forest (d).