

# Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages

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## ABSTRACT

Global biodiversity is changing rapidly driven by human alteration of habitat, and nowhere this is more dramatic than in insular habitats. Yet land-cover change is a complex phenomenon that not only involves habitat destruction but also forest recovery over different time scales. Therefore, we might expect species to respond in diverse ways with likely consequences for the reorganization of regional assemblages. These changes, however, may be different in tropical islands because of their low species richness, generalist habits and high proportion of endemics. Here, we focus on the island of Puerto Rico and ask how island-wide changes in land cover and land use has influenced the large-scale organization of bird assemblages. To address this question, we combined in a Geographical Information System (GIS) the first 6 years (1997–2002) of the Puerto Rican Breeding Bird Survey (PR-BBS) with land-cover and land-use data extracted from a published digital map derived from the classification of Landsat images. A Non-metric Multidimensional Scaling (NMS) ordination based on the composition and abundance of birds, and percentage land-use types showed that land use followed by climate could explain most of the variation observed among routes in terms of species composition and abundance. Moreover, endemic and exotic species were widely distributed throughout the island, but the proportion of endemic species is higher in closed forests while exotic species are more abundant in open habitats. However, historical accounts from the early 1900s indicate that endemic species were distributed across the entire island. Today, most of the land cover transformation in Puerto Rico occurs in the lowlands which may explain the high abundance of endemic species in cloud forests and the high abundance of exotic species in open habitats in the lowlands.

## Keywords

Biological invasions, bird assemblages, endemic species, land cover, land use, Puerto Rico.

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## INTRODUCTION

Global biodiversity is decreasing rapidly, driven by human alteration of habitat (Pimm *et al.*, 1995; Sala *et al.*, 2000) and the resulting complex mosaic of land covers (Grau *et al.*, 2003; Lambin *et al.*, 2003). This mosaic of land covers may interact with the habitat requirements of species to determine the large-scale reorganization of species assemblages, including the persistence and extinction of native and endemics, and the spread of exotics (Keitt & Stanley, 1998; Brown *et al.*, 2001).

The effect of land-cover and land-use change on the large-scale organization of species assemblages may be stronger in islands (Brooks *et al.*, 1997; Blackburn *et al.*, 2004; Mittermeier *et al.*,

2005). Islands have fewer species than continents, but proportionally more endemics (Cox & Ricklefs, 1977). Moreover, during historic times 90% of the birds that have gone extinct are island endemics (Johnson & Stattersfield, 1990). The causes of these extinctions are diverse, but most included habitat destruction, hunting pressure and the introduction of exotic species (e.g. predators and browsers) (Johnson & Stattersfield, 1990; Brooks *et al.*, 1997; Blackburn *et al.*, 2004).

Islands are especially vulnerable to the introduction of exotic birds (Simberloff, 1995) and 70% of all reported bird introductions have occurred in islands (Blackburn & Duncan, 2001). Two hypotheses have been suggested to explain the vulnerability of islands to invasion by exotic species. One possibility is that they

are more vulnerable because of low species richness, absence of certain functional groups (e.g. predators) and increased landscape transformation (Perrings *et al.*, 2000; Duncan *et al.*, 2001). Alternatively, exotics may be more common on islands simply because of the many attempts to introduce them on islands (Duncan *et al.*, 2001). Both hypotheses agree on the importance of human-induced changes in aiding invasion. Less clear are the possible consequences of exotics on native species. Some studies suggest that exotic species have a detrimental effect on native avifauna (Green, 1984; Temple, 1992). Others argue that the effect is minimal since most exotics establish in highly modified habitats which are rarely used by native species (Case, 1996; Duncan *et al.*, 2001).

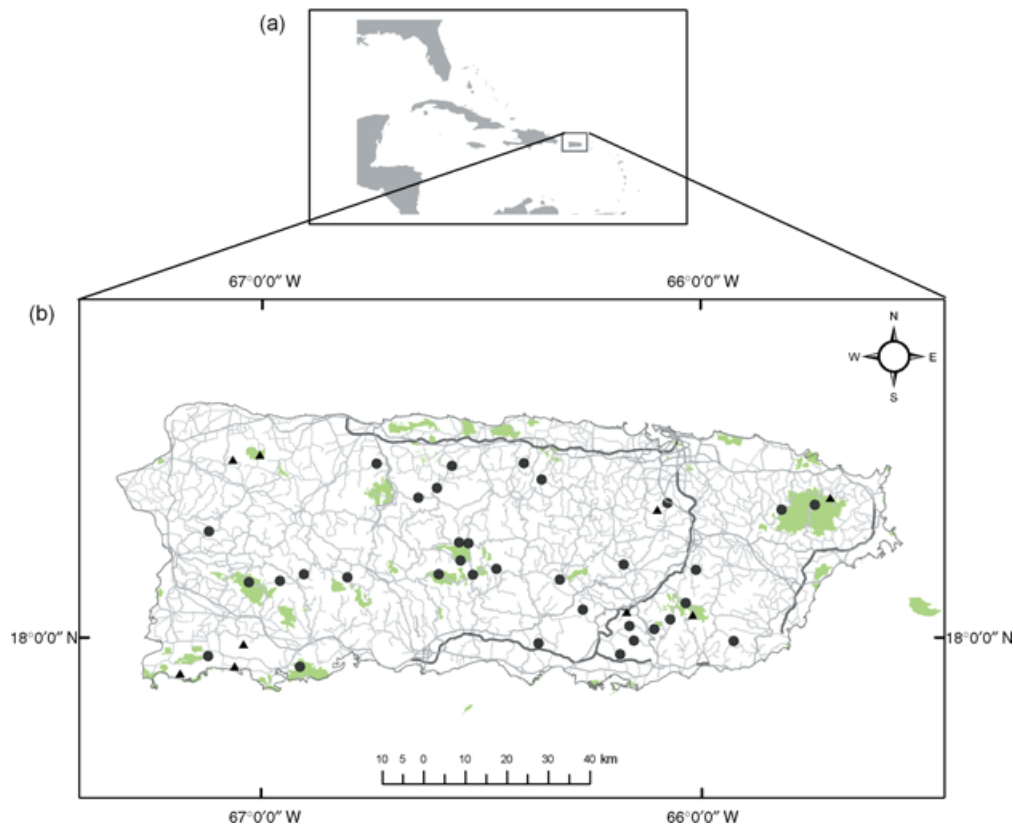
To better understand the effect of land-cover and land-use change, and the introduction of exotic species on an insular avifauna, we studied bird species composition and its relationship with land-cover and land-use variables in the island of Puerto Rico. Puerto Rico, the smallest of the Greater Antilles, represents an interesting and well-documented case of regional changes in land-cover and land-use change in the tropics (Grau *et al.*, 2003; Aide & Grau, 2004). Although closed forests covered roughly 42% of the island in 1991–92 (Helmer *et al.*, 2002), this was not the case in the early 1900s when only 7% of the island was under forest cover (Dietz, 1986). In the early 1900s sugar cane plantations dominated the lowlands, coffee dominated the mountains

while pastures were distributed throughout the island (Dietz, 1986; Dominguez-Cristóbal, 2000). In 1952, a change in the political status of Puerto Rico shifted socio-economic activities from agriculture to a manufacture-based economy (Dietz, 1986). Many agricultural fields were abandoned and forests started to recover. Today these secondary forests are widely distributed throughout the island (Helmer *et al.*, 2002) but are now threatened by urban expansion (López *et al.*, 2001). Here, we investigate how the present state of land cover and land use is influencing the large-scale organization of Puerto Rico's bird assemblages. Specifically we ask: (1) How do the composition and abundance of birds across Puerto Rico relate to current patterns of land cover and land use? and (2) How are native, endemic and exotic species responding to these large-scale changes?

## METHODS

### Study site

Puerto Rico is a subtropical island with an area of c. 8900 km<sup>2</sup> and maximum elevation of c. 1300 m (Fig. 1a). Although relatively small it has a wide diversity of climates represented by six life zones, ranging from lowland dry to subtropical rain forests (Ewel & Whitmore, 1973). Superimposed on this diverse array of life zones, is an equally diverse array of land covers and land uses,



**Figure 1** (a) Greater Antilles showing the island of Puerto Rico. (b) Puerto Rican Breeding Bird Survey (PR-BBS) routes distinguishing between those included in the analyses (black circles) and those excluded (black triangles). Puerto Rico's road network includes highways, primary, secondary and tertiary roads. These are shown as lines of different thickness. Puerto Rico's protected areas appear in green.

**Table 1** Land-cover/land-use types used in this study are based on a reclassification of Helmer's *et al.* (2002) types.

Land-cover/land-use classes in this study	Land-cover/land-use classes in Helmer <i>et al.</i> (2002)	Puerto Rico (%)	Routes (%)
Forest*	Lowland dry: (1) semi-deciduous forest; and (2) woodland/shrubland Lowland dry mixed evergreen drought-deciduous shrubland with succulents Lowland dry and moist, mixed seasonal evergreen sclerophyllous forests Lowland moist: (1) evergreen hemi-sclerophyllous shrubland; (2) seasonal evergreen forest; (3) seasonal evergreen forest/shrubland; (4) coconut palm forest; (5) semi-deciduous forest; (6) semi-deciduous forest/shrubland; (7) seasonal evergreen and semi-deciduous forest; and (8) seasonal evergreen and semi-deciduous forest/shrub Submontane wet evergreen forest. Submontane and lower montane wet evergreen: (1) sclerophyllous forest; (2) sclerophyllous forest/shrub; (3) forest/shrubland; and active/abandoned shade coffee Lower montane wet evergreen forest: (1) tall cloud forest; (2) mixed palm and elfin cloud forest; and (3) elfin cloud forest	41	52
Coffee	Active sun/shade coffee, submontane and lower montane wet forest/shrubland, other agriculture (orchards)	3	5
Wetland	Tidally and semi-permanently flooded evergreen sclerophyllous forest Tidally flooded evergreen dwarf-shrubland and forb vegetation Seasonally flooded rain forest Other emergent wetlands (including seasonally flooded pasture) Salt and mudflats	2	< 1
Water	Water	1	< 1
Pasture*	Pasture	37	34
Agriculture*	Agriculture/hay and agriculture	6	3
Urban and barren	Urban and barren	11	6
Quarries	Quarries	< 1	< 1

Under Puerto Rico and Routes is the percentage of each land-cover/land-use type. Land-cover/land-use type that were statistically significant in the ordination analysis are marked with an (\*).

which includes closed forests in various stages of succession, pastures, agricultural fields, quarries, suburban and urban areas (Table 1; Helmer *et al.*, 2002).

The avifauna of the island comprises 16 endemic, 88 native, 49 exotic, 102 migratory and 104 vagrant species (Biaggi, 1997; Oberle, 2003; M. W. Oberle, unpubl. data). All of the endemic species, most of the exotic species, and half of the native, migratory and vagrant species are associated with terrestrial habitats. Currently, three Puerto Rican endemic bird species are in decline and are listed as threatened (IUCN, 2004); in contrast several native-habitat generalists and exotics have expanded their range on the island (Raffaele, 1989; Camacho Rodríguez *et al.*, 1999).

### Bird composition and abundance

To determine the relationship between land-cover and land-use variables, and bird species composition, we used bird composition and abundance data generated by the Puerto Rican Breeding Bird Survey (PR-BBS; [http://www.pwrc.usgs.gov/bbs/Puerto\\_Rico](http://www.pwrc.usgs.gov/bbs/Puerto_Rico)). The PR-BBS is a long-term monitoring program that started in 1997, similar to the Bird Breeding Surveys (BBS) of the United States and England (Peterjohn, 1994). By counting birds at the same locations through time (Link & Sauer, 1998) the PR-BBS seeks to monitor the status and trends of Puerto Rican breeding

bird populations over large areas and periods of time (Pardieck & Peterjohn, 1997). In Puerto Rico, the surveys take place each year between 15 April and 15 May along routes distributed across the island (Fig. 1b). Each route is an 8-km section of a road where trained observers conduct 5-min point counts every 0.8 km and record every bird heard or seen within a 200-m radius (Pardieck & Peterjohn, 1997; route maps and bird data provided by E. Hernandez-Prieto). We added for each route all observations from the 11 point counts.

Between 1997 and 2002, 43 routes were censused by the PR-BBS, but our analysis was limited to 34 routes running through terrestrial habitats and for which there were detailed directions. This information was crucial for geocoding and characterizing the routes in terms of percentage land-cover and land-use types. Not all routes were censused every year. The number of censuses in each route varied from one to six censuses. We examined the cumulative species-sampling effort curves, and 10 of the routes that were censused three or more times approached an asymptotic behaviour (Supplementary Fig. S1). Routes that were censused only once had species richness values that were in the range of the initial values of those routes that had been censused two or more times. These routes were also included in the analysis because they provided invaluable information on regions not covered by other routes. Given the uneven sampling of the

routes in time we limit our analyses to the study of bird species composition and its association with land-use variables as composite covering the period 1997–2002. Therefore, we averaged the yearly species counts for each route censused two or more times to estimate relative bird abundances.

### Routes and landscape characteristics

Each route was characterized in terms of Holdridge life zones (Ewel & Whitmore, 1973) and the abundance of land-use types based on a digital map produced by Helmer *et al.* (2002). This map is based on a supervised classification of Landsat TM images (1991–92) that were previously segmented using a map of Puerto Rico's ecological life zones *sensu* Holdridge and geology. Within each life zone Helmer *et al.* (2002) used aerial photographs and ground-truthing to collect training signatures representing land-cover and land-use types based on the percentage of woody vegetation and leaf phenology. In total, 33 land-cover and land-use types were identified, but for our study we merged these into eight categories (Table 1) to separate the effect of life zones and land use. In addition, merging land-cover and land-use types reduced the dimensionality of the data and the number of zeros in the data matrix. The proportion of each of the eight land-use categories was similar between PR-BBS and the whole island (Table 1). The only exception was the 'forest' category, which was slightly over represented in the routes when compared to the island as a whole.

In a Geographical Information System (GIS), we generated a PR-BBS route coverage using information on route location (E. Hernández-Prieto, unpubl. data). Since bird point counts are conducted within a radius of 200-m, we constructed a 200-m wide buffer around each 8-km long route. Given the high density of roads that characterizes the island and its current suburban nature, this 200-m is likely to be the representative of what is found beyond the area encompassed by this buffer (López *et al.*, 2001). This map was overlaid over the reclassified map of land-cover and land-use types to extract information on the number of pixels present for each land-use type. These figures were later transformed into percentage cover.

### Data analysis

Non-metric Multidimensional Scaling (NMS) was used to ordinate PR-BBS routes based on bird species composition and abundance, and to establish relationships with land-cover and land-use types. The primary matrix characterizes each route based on the average number of bird counts for a given species and route over time, whereas the secondary matrix by the percentage of each land-cover and land-use type within each route. NMS makes an iterative search for the least stress position of data on  $k$ -dimensions based on ranked similarity distances (McCune & Grace, 2002). It has several advantages over other ordination methods (e.g. Principal Components Analysis (PCA), Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA)) because it does not assume linearity of the data and it does not require data transformation (Clarke, 1993). In addition, the inclusion of covariates can also

be evaluated which in our case was represented by the percentage of land-cover and land-use types (Quinn & Keough, 2002). Given these advantages, it has been proposed as the most appropriate ordination method for ecological data (Clarke, 1993). We used the Sørensen index as the distance measure, a random starting configuration with a maximum of six axes, stability criterion =  $5 \times 10^{-5}$ , 50 permutations with real data and Monte Carlo test based on 50 permutations. The final number of dimensions in the solution and its stability were determined by a combination of results from Monte Carlo tests, examination of NMS plots and solutions with minimum number of dimensions that provided the lowest stress and instability (McCune & Grace, 2002). All ordination analyses were done using PC ORD 4.

To establish differences in the proportion of exotic and endemic species between low elevation and drier to moist life zones (lowland dry forest and lowland moist forest), and high elevation and wetter life zones (lowland wet forest, lowland rain forest and lower montane wet forest) we performed a Mann–Whitney  $U$ -tests.

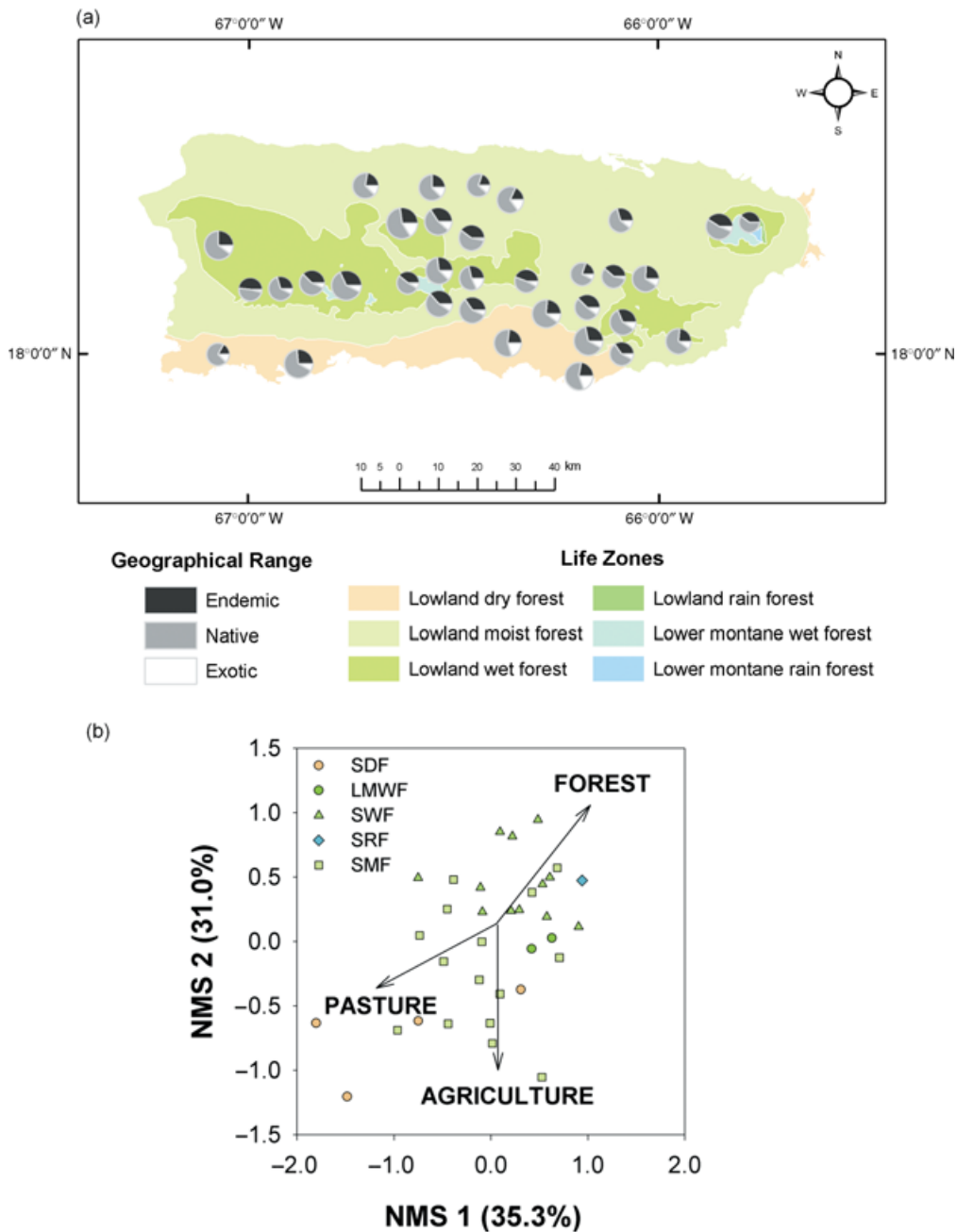
### RESULTS

A total of 86 species were recorded by the PR-BBS between 1997 and 2002 (Supplementary Appendix S1). Of these, 14 species are endemic, 55 native and 15 exotic to the island of Puerto Rico; two species, the osprey (*Pandion haliaetus*), and barn swallow (*Hirundo rustica*) are migratory (Supplementary Appendix S1). The species recorded by the PR-BBS represent 93% (endemic and natives) or 65% (endemics, natives and exotics) of Puerto Rico's terrestrial avifauna. The remaining species (i.e. non-terrestrial species) reported by the PR-BBS are characteristic of wetlands, and were found mostly along routes in the vicinity of human-made reservoirs found in the mountains.

#### Island-wide bird assemblages

Bird species richness of the PR-BBS routes varied from 23 to 52 species. All routes included native and endemic species (Fig. 2a). Exotic species were also widely distributed throughout most routes, with the exception of a route located in the Caribbean National Forest (Fig. 2a). We found that the proportion of exotic species was significantly higher in low elevation, drier life zones (lowland dry forests and lowland moist forests;  $W = 568.5$ ,  $P = 0.002$ ), while the proportion of endemic species was significantly greater in high elevation and wetter life zones (lowland wet forest, lowland rain forest and lower montane wet forest;  $W = 236.5$ ,  $P < 0.0005$ ).

The NMS ordination of PR-BBS routes extracted three axes and we used the two that explained the largest proportion of the total variance (66.3%). Routes varied in terms of bird species composition and abundance (Fig. 2b), and this seems to reflect the dominance of forest in some routes vs. open habitats (agriculture and pastures) in others. Forest was positively correlated with axes 1 and 2 of the NMS ( $r_{\text{NMS1}} = 0.572$ ,  $r_{\text{NMS2}} = 0.369$ ) whereas pasture ( $r_{\text{NMS1}} = -0.465$ ,  $r_{\text{NMS2}} = -0.468$ ) and agriculture ( $r_{\text{NMS2}} = -0.351$ ) were negatively correlated with these axes



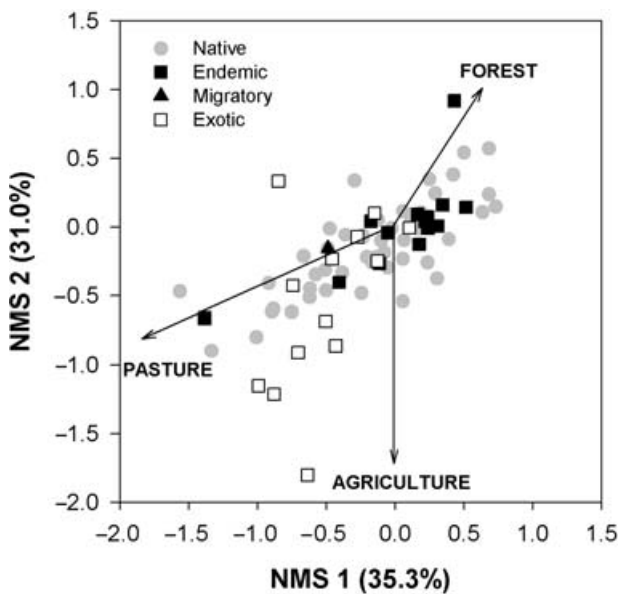
**Figure 2** (a) Life zone map of Puerto Rico showing species composition in terms of the proportion of native, endemic and exotic species. The size of the circles denotes species richness. (b) NMS ordination showing the relationship between routes and land-use types. Points indicate routes classified according to life zone (SDF, subtropical lowland dry forest; SMF, subtropical lowland moist forest; SRF, subtropical lowland rain forest; SWF, subtropical lowland wet forest; and LMWF, subtropical lower montane wet forest).

( $P < 0.05$ ). When we overlay information on life zones, we see a gradient-like distribution from routes located at higher wetter sites (lowland rain forest, lowland wet forest and lower montane wet forest), to lower drier sites (lowland moist forest and lowland dry forest; Fig. 2b).

### Endemic and exotic bird species

The ordination of species showed a gradient in which endemic species seemed associated with forests and high elevation, wetter

life zones and exotics with disturbed habitats and low elevation, drier zones (Fig. 3). In contrast, native species were found across the ordination space. Most of the island endemic species had positive values along both axes. On the other hand, most of the exotic species ( $n = 14$ ; Supplementary Appendix S1) showed negative values along both axes and were associated with open, disturbed habitats such as pasture and agriculture (Fig. 3). An exception was the shiny cowbird, which was located in the ordination in the closed-canopy forest habitat (Supplementary Appendix S1; Fig. 3). Given that PR-BBS censuses take place



**Figure 3** NMS ordination based on bird species composition including correlations with land-cover/land-use types indicated as vectors. Points represent species classified into four classes (exotic, endemic, native and migrant species). Most endemics are located in the portion of the ordination diagram that corresponds to closed forest and most exotic species are located near disturbed habitats (pasture and agriculture). Native species are distributed along the whole ordination diagram.

along roadsides, we expect its occurrence in this portion of ordination space since this species is common along forest edges. The common ground-dove ( $r_{\text{NMS1}} = -0.485$ ,  $r_{\text{NMS2}} = -0.682$ ), Greater Antillean grackle ( $r_{\text{NMS1}} = -0.555$ ,  $r_{\text{NMS2}} = -0.696$ ), grey kingbird ( $r_{\text{NMS1}} = -0.658$ ,  $r_{\text{NMS2}} = -0.515$ ), northern mockingbird ( $r_{\text{NMS1}} = -0.527$ ,  $r_{\text{NMS2}} = -0.722$ ) and mourning dove ( $r_{\text{NMS1}} = -0.405$ ,  $r_{\text{NMS2}} = -0.371$ ), are native species with significant ( $P < 0.05$ ) negative correlations with both ordination axes. Exotic species which significantly correlated with both axis were the house sparrow ( $r_{\text{NMS1}} = -0.447$ ,  $r_{\text{NMS2}} = -0.440$ ), and pin-tailed whydah ( $r_{\text{NMS1}} = -0.350$ ,  $r_{\text{NMS2}} = -0.410$ ). None of the endemic species was significantly correlated with both axes. The Puerto Rican bullfinch ( $r_{\text{NMS1}} = 0.368$ ), Puerto Rican woodpecker ( $r_{\text{NMS1}} = 0.529$ ), Puerto Rican tody ( $r_{\text{NMS1}} = 0.587$ ), Puerto Rican tanager ( $r_{\text{NMS1}} = 0.545$ ), Puerto Rican spindalis ( $r_{\text{NMS1}} = 0.501$ ) and Puerto Rican emerald ( $r_{\text{NMS1}} = 0.377$ ) were significantly correlated with axis 1. On the other hand, the Elfin Woods warbler ( $r_{\text{NMS2}} = 0.359$ ) was positively correlated with axis 2, whereas the Adelaide's warbler ( $r_{\text{NMS2}} = -0.355$ ) and Puerto Rican flycatcher ( $r_{\text{NMS2}} = -0.467$ ) were negatively correlated (Supplementary Appendix S1; Fig. 3).

## DISCUSSION

The large-scale composition and abundance of bird assemblages across the island of Puerto Rico seems to be correlated with land use followed by climate. Moreover, endemic and exotic species are widely distributed throughout the island, but the proportion

of endemic species is higher in closed forests while exotic species are more abundant in open habitats. Currently most closed-canopy forest habitats are found at high elevations whereas open habitats dominated by pastures and agricultural fields are found at low elevation, mainly in dry to moist life zones.

Large-scale biotic data are crucial for accurate management and conservation decisions, but given the difficulty of collecting data over large spatial and temporal scales, this kind of data is often scarce. The PR-BBS is an effort aimed at collecting this kind of large-scale data, but it has some limitations that include irregular sampling and observer bias. Even though these limitations, the PR-BBS includes routes across the entire island, allowing the large-scale characterization of patterns of bird species composition and abundance.

One of these large-scale patterns was the presence of endemic, exotic and native species across all PR-BBS routes, regardless of land use or life zone (Fig. 3). Bird species on islands show less habitat differentiation, that is, occupy a greater diversity of habitats than do continental species (Cox & Ricklefs, 1977). Studies conducted in other parts of the West Indies, New Guinea and the Mediterranean have suggested that low bird species richness on islands results in generalist behaviour in habitat use and niche expansion (Terborgh *et al.*, 1978; Wright, 1980; Blondel *et al.*, 1988). Although island birds are usually characterized as generalists, some species in our study had strong and specific habitat preferences. For example, exotic species were generally more abundant in disturbed areas, while endemic species were much more abundant in forested habitats. Furthermore, some native species have potentially benefited from the increase of disturbed areas as may have happened with the common ground-dove, Greater Antillean grackle, grey kingbird, northern mockingbird and mourning dove which are known to be generalists not only in terms of habitat use but also in terms of diet and nesting requirements. These species were highly correlated with both NMS axes and were located in the ordination space that corresponded to disturbed habitats (Fig. 3).

Although endemic, exotic and natives bird species occurred in all habitats, the actual species composition varied between forested sites and disturbed habitats (pasture and agriculture), and between high elevation wetter life zones and low elevation drier life zones. Today most of the high input agriculture, cattle ranching and urban developments are found in the lowland dry and moist life zones, especially in coastal areas. In contrast, secondary forests dominate life zones at high elevations (Grau *et al.*, 2003).

The above observations raise two questions. First, to what extent have humans contributed to the expansion and contraction of the geographical ranges of exotic and endemic species in the island? Second, to what extent have human activities confined endemic species to a limited set of protected areas? In the early 1900s more than 7% of the island was covered by closed forest, while the rest was devoted to agriculture (Dietz, 1986; Dominguez-Cristóbal, 2000). There are reports of the extinction of at least four bird species during historic times (*Aramus guarauna*, *Phoenicopterus ruber*, *Corvus leucognaphalus* and *Aratinga chloroptera maugaei*) (Wiley, 1996; Biaggi, 1997), and of 10 other

species, nine of which endemic to the island, during the late Pleistocene/Holocene (Wetmore, 1922; Pregill & Olson, 1981; Olson, 1982; Olson & McKittrick, 1982; Biaggi, 1997). On the other hand, by the early 1900s only six exotic species had been recorded in the island, two of which are no longer present and a third (helmeted guineafowl) is now rare in the wild. In contrast, the number of known exotic species in the island today is 49 (Camacho Rodríguez *et al.*, 1999). It has been suggested that this increase in the number of exotic species (from 6 to 49) is a product of landscape modifications, and an increase in legal and illegal pet trade. The widespread distribution of cattle egrets and shiny cowbirds across the island is an example of the positive effects of landscape modification on the spread of exotic species (Post & Wiley, 1977; Biaggi, 1997). Moreover, the shiny cowbird is a brood parasite of yellow-shoulder blackbirds, an endemic species that is currently endangered. The spread of the pin-tailed whydah and troupial are product of the increase of the pet trade in the 1960s and 1970s (Raffaele, 1989). In contrast, endemic bird species rarely use disturbed habitat such as sugar cane plantations or pastures, thus these species in the early 1900s were restricted to forest and coffee plantations that represented more than 7% of the total area of the island.

Our results and the above accounts suggest that the avifauna of Puerto Rico has reorganized in response to the direct and indirect effects of human activities. Species richness has increased due to the colonization of exotic species. In addition, endemic species are today widely distributed throughout the island, demonstrating that they have re-colonized some of the new secondary forests, yet they are still more abundant in the mountains. In contrast, abandoned agricultural lands in the lowlands are increasingly converted into urban areas (Lopez *et al.*, 2001). Given their lack of vertical forest structure, urban areas are difficult to colonize by forest interior birds (Blair, 1996) but are easily colonized by exotics (Duncan *et al.*, 2001).

Similar results have been found elsewhere in the tropics. In the surroundings of Lore Lindu National Park in Sulawesi, species richness was similar among primary and secondary forest, and mixed-rural habitats, but very different from rubber plantations (Sodhi, 2005). An ordination of sites based on bird species composition, however, separated the mixed-rural habitats and rubber plantations from forested sites. In another example, the densely populated island of Singapore offers an interesting comparison with Puerto Rico. Roughly, a fourth of the area of Puerto Rico, Singapore's land-use history mirrors to some extent that of Puerto Rico (Corlett, 1992). Unlike Puerto Rico, however, the transition from an agricultural to an industrial economy was not followed by a large-scale recovery of forest cover. Instead, former agricultural lands were converted to urban areas that today occupy 50% of the island (in Puerto Rico they represent 11%) (Corlett, 1992; Helmer *et al.*, 2002). Around 30% of Singapore's bird species are now locally extinct (total number varies depending on author and ranges between 203 and 383) and most of which were forest-dependent species (Corlett, 1992; Castelletta *et al.*, 2000, 2005). In addition, around 18 exotic species have been established. The colonization of newly modified sites by exotic species is consistent with our findings. In contrast, even

though Singapore and Puerto Rico have both undergone large-scale landscape transformations, 30% of Singapore's bird species have gone extinct while in Puerto Rico this loss is < 1%. Three possible hypotheses may explain the observed discrepancies. First, Puerto Rico may have lost many more species than recognized but we do not know about them because of the scarcity of studies conducted in the island during the Spanish occupation. This lack of historical information has also been recognized as an important issue for the estimation of global bird extinctions (Pimm *et al.*, 2007). Second, the large-scale recovery of forest cover contributed to that of birds. Third, the Puerto Rican avifauna may be resilient to forest change due to the high incidence of hurricanes in the Caribbean (Wunderle *et al.*, 1992).

Our work is the first for any island in the Caribbean to document the reorganization of bird communities at a regional scale, that is, the scale of the island of Puerto Rico. Results from our study and others discussed above, clearly indicates that land-use change is behind the large-scale reorganization of bird assemblages. This reorganization includes the global and local extinction of some species, colonization of exotics and the shift of species distributions. This shift may be positive for forest interior species, if land-use changes are joined by forest recovery as is the case of Puerto Rico, but it can also be negative if forest is converted to urban development as is the case of Singapore.

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## SUPPLEMENTARY MATERIAL

The following supplementary materials are available for this article:

**Figure S1** Cumulative species-sampling effort curves for the 34 PR-BBS routes included in this study.

**Appendix S1** Bird species detected by the PR-BBS (1997–2002) including geographical range, conservation status and ordination scores.

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