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# The influence of dispersal on macroecological patterns of Lesser Antillean birds

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## ABSTRACT

**Aim** Dispersal is often assumed to be a major force in shaping macroecological patterns, but this is rarely tested. Here I describe macroecological patterns for two groups of Lesser Antillean birds and then use population genetic data to assess if differences in dispersal ability could be responsible for the groups' contrasting patterns. Importantly, the population genetic data are derived independently from any data used to generate the macroecological patterns.

**Location** The Lesser Antilles, Caribbean.

**Methods** I used data from the literature to construct species–area curves and evaluate the decline in species compositional similarity with geographic distance (hereafter distance–decay) for two sets of bird communities in the Lesser Antilles, those found in rain forest and those in dry forest. I then used mitochondrial DNA sequences from island populations to assess the dispersal ability of rain forest and dry forest species.

**Results** Rain forest species show steeper species–area curves and greater distance–decay in community similarity than dry forest species, patterns that could be explained by rain forest species having more limited dispersal ability. Both conventional analyses of $M$, the number of migrants per generation between populations, and alternative analyses of $D_A$, the genetic distance between populations, suggest that rain forest species disperse between islands less frequently than dry forest species.

**Main conclusions** Differences in dispersal ability are a plausible explanation for the contrasting macroecological patterns of rain forest and dry forest species. Additionally, historical factors, such as the taxon cycle and Pleistocene climate fluctuations, may have played a role in shaping the distribution patterns of Lesser Antillean birds.

**Keywords**

**Birds, Caribbean, community similarity, dispersal, distance–decay, island biogeography, macroecology, spatial pattern, species–area relationship, taxon cycle.**

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## INTRODUCTION

Dispersal can have a profound effect on macroecological patterns such as species–area relationships and distance–decay, the decline in similarity in species composition of communities with geographic distance (Gaston & Blackburn, 2000). For example, if dispersal is unlimited and no other factors affect distribution, all species should be found everywhere and there will be no relationship between area and species diversity. Conversely, theory predicts that reduced dispersal should increase the $z$-value, or power-law exponent, of the species–area relationship because local extinctions, which are more probable in smaller areas, are not readily replaced through recolonization (MacArthur & Wilson, 1963, 1967; Bell, 2001; Hubbell, 2001; Chave *et al.*, 2002). Reduced dispersal should also increase distance–decay in community similarity, because

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high dispersal is the primary means by which community similarity is maintained in the face of differential local extinctions and potential allopatric speciation (Bell, 2001; Hubbell, 2001; Chave & Leigh, 2002; Mouquet & Loreau, 2003; Morlon *et al.*, 2008). Early investigations of the role of dispersal in shaping macroecological patterns often focused on island systems (e.g. MacArthur & Wilson, 1963, 1967; Terborgh, 1973; Diamond & Mayr, 1976), while most recent theoretical developments have concerned mainland environments (all citations post-2000 above). Nevertheless, island archipelagos continue to serve as model systems in macroecology (Rosenzweig, 1995; Gaston & Blackburn, 2000; Whittaker & Fernández-Palacios, 2007), and most of the recent theoretical predictions from mainland environments apply to islands as well.

A recent simulation study demonstrated that, within the same archipelago, poorly dispersing taxa should have steeper species–area curves than well dispersing taxa (Hovestadt & Poethke, 2005). This result has also been found empirically in studies comparing volant versus non-volant animals (Wright, 1981; Lomolino, 1984). Diamond & Mayr (1976) classified bird species according to their dispersal ability, and showed that putatively poorly dispersing sets of bird have steeper species–area curves. Given that birds do not differ in any conspicuous way that relates to their dispersal abilities (as volant and non-volant animals do), Diamond & Mayr (1976) instead assessed dispersal ability through examining distribution patterns (Diamond, 1975). However, this is circular, because community-level macroecological patterns, such as species–area curves, stem directly from species-level distribution patterns. Other factors besides dispersal, such as habitat specialization or extinction, can also shape a species' distribution. Therefore, it may be erroneous to conclude that dispersal affects macroecological patterns when dispersal has been assessed solely based on distribution patterns. Many other studies have concluded that dispersal affects the form of species–area curves (e.g. Brown, 1971; Terborgh, 1973; Strong & Levin, 1975) without estimating dispersal in any rigorous manner (Connor & McCoy, 1979). Likewise, the rate of distance–decay in community similarity has been interpreted in terms of dispersal in cases where no attempts to estimate dispersal were made (e.g. Nekola & White, 1999; Condit *et al.*, 2002). In order to validate a role for dispersal in shaping macroecological patterns, empirical studies are needed that estimate dispersal rates independently from the data used to elucidate the patterns.

There is a long history of macroecological studies of Lesser Antillean bird communities (Ricklefs & Cox, 1972, 1978; Terborgh, 1973; Terborgh *et al.*, 1978; Terborgh & Faaborg, 1980; Faaborg, 1982, 1985; Gotelli & Abele, 1982; Case *et al.*, 1983; Ricklefs & Bermingham, 1999, 2001, 2002, 2004a; Ricklefs & Lovette, 1999), which makes these communities a fertile ground for examining how dispersal can affect macroecological patterns. Ricklefs and colleagues (Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2004a) have explained contrasting species–area curves in Lesser Antillean birds as part of the taxon cycle hypothesis, under which species initially colonize all islands and then cease to disperse between islands. They argue that old colonists have a steeper species–area curve than recent colonists because they have had more time to go extinct on individual, usually smaller, islands (for the purpose of simplification, I here refer to the restricted endemics of Ricklefs & Bermingham, 2004a, as old colonists and to the young species and widespread endemics as recent colonists). This hypothesis emphasizes the role of extinction in generating patterns, but the role of inter-island dispersal after colonization, while discussed (Ricklefs & Bermingham, 2004a), has not been adequately explored. Furthermore, Ricklefs & Bermingham (2004a) used genetic distance estimates between Lesser Antillean and source populations (in the Greater Antilles or South America) or among Lesser Antillean populations themselves to classify species as old versus recent colonists (Ricklefs & Bermingham, 2001), and these estimates can also be affected by dispersal rates. The putative recent colonists may simply be species with high dispersal rates (both into and within the archipelago), while putative old colonists may be species with low dispersal rates (Cherry *et al.*, 2002; Ricklefs & Bermingham, 2004b).

The putative old colonists of Ricklefs and colleagues are principally found in interior rain forest habitats while the recent colonists are found in peripheral dry forest habitats (Ricklefs & Bermingham, 2004a). Terborgh and colleagues have previously suggested that rain forest species in the Lesser Antilles disperse between islands less frequently than dry forest species, based on their contrasting distribution patterns (Terborgh *et al.*, 1978; Terborgh & Faaborg, 1980). Rain forest species are often absent from islands with rain forest habitat, while dry forest species are present nearly everywhere there is dry forest. Rain forest habitat does not differ greatly between islands, and it does not seem that the distribution or characteristics of rain forest habitat itself are responsible for these absences (Ricklefs & Cox, 1978; Terborgh & Faaborg, 1980; Ricklefs & Lovette, 1999). Nevertheless, as discussed above, inferring dispersal rates based solely on distribution patterns can be problematic, as many other factors besides dispersal can shape distribution patterns (e.g. increased extinction probabilities). The role of inter-island dispersal in shaping macroecological patterns in Lesser Antillean birds is unresolved (Cherry *et al.*, 2002; Ricklefs & Bermingham, 2004b), and a fresh examination of these patterns is warranted, particularly in integration with rigorous estimates of dispersal.

In this study, I examine macroecological patterns, specifically species–area curves and distance–decay in community similarity, for dry forest and rain forest Lesser Antillean bird communities. While many authors have constructed species–area curves for different classes of Antillean birds (Ricklefs & Cox, 1972; Terborgh, 1973; Terborgh & Faaborg, 1980; Faaborg, 1985; Ricklefs & Lovette, 1999; Ricklefs & Bermingham, 2004a), no study has explicitly contrasted these curves for dry forest and rain forest communities. Likewise, distance–decay in community similarity has been examined in Lesser Antillean bird communities (Terborgh, 1973), but dry forest and rain forest patterns of distance–decay have not been compared. Here, I show that rain forest communities have a steeper species–area curve and greater distance–decay in community similarity. Based on this, I predict, like Terborgh and colleagues (Terborgh *et al.*, 1978; Terborgh & Faaborg, 1980), that rain forest species disperse between islands less frequently than dry forest species do. I then take advantage of the remarkable phylogeographic data set that Ricklefs & Bermingham (2001) have assembled for Lesser Antillean birds (mitochondrial sequence data are available from multiple islands for half the dry forest and over half the rain forest species) to determine if differential inter-island dispersal can be responsible for the observed contrast in macroecological patterns. Importantly, the phylogeographic data are derived independently from species distribution data and thus provide a powerful alternative means for assessing the role of dispersal in shaping macroecological patterns.

## MATERIALS AND METHODS

### Study system and data sources

The Lesser Antilles extend south-eastward from Puerto Rico and the Greater Antilles to the northern coast of Venezuela. The two principal habitats in the Lesser Antilles are lower-elevation dry forest (sclerophyll scrub) and higher-elevation rain forest (Terborgh *et al.*, 1978; Faaborg, 1985). Faaborg (1985) and Ricklefs & Bermingham (2004a) give the island distributions and habitat preference for Lesser Antillean bird species; birds are classified as rain forest, dry forest, generalist or miscellaneous species (the latter utilize rare habitats such as stream banks or mangroves). I constructed lists of species specific to rain forest and dry forest for all possible islands ($n = 13$ islands for rain forest, $n = 16$ for dry forest). Generalist species and those with a miscellaneous habitat preference were excluded from habitat-specific species lists.

I obtained the Ricklefs & Bermingham (2001) mitochondrial DNA sequence data (ATPase 6 and 8 genes; 842 bp in total) from multiple island populations for eight of 16 total dry forest species and 13 of 24 total rain forest species (see Table 1 for species and GenBank accession numbers). Island populations are represented by 1–14 sequenced individuals, with most represented by two individuals (69 of 91).

### Distribution analyses

While others have noted that rain forest species occupy fewer islands than dry forest species (Ricklefs & Cox, 1978; Terborgh *et al.*, 1978), it was of interest to determine if this difference is statistically significant. For each species, I computed the fraction of islands with suitable habitat that are occupied. I also counted how frequently a given species is absent from an island with suitable habitat when the species is present on a neighbouring island. The first metric can signify global dispersal limitation while the latter can assess how limited dispersal is between neighbouring islands. I compared dry forest and rain forest species for both metrics using a Mann–Whitney *U*-test.

**Table 1** Species used in genetic analyses of dispersal rates, their habitat preference in the Lesser Antilles and GenBank accession numbers of sequences used. Nomenclature follows Ricklefs & Bermingham (2004a; American Ornithologist's Union).

| Species | Habitat | Accession numbers |
|---|---|---|
| *Columbina passerina* | Dry forest | AF132377–AF132382,<br>AF485048–AF485063 |
| *Dendroica petechia* | Dry forest | AY115296–AY115306 |
| *Elaenia martinica* | Dry forest | AF1323838–AF132388,<br>AY082535–AY082548 |
| *Eulampis holosericeus** | Dry forest | AY082564–AY082572 |
| *Mimus gilvus* | Dry forest | AF140960–AF140974 |
| *Saltator albicollis* | Dry forest | AY115270–AY115278 |
| *Tiaris bicolor* | Dry forest | AF132428–AF132433 |
| *Tyrannus dominicensis* | Dry forest | AY115258–AY115268 |
| *Cinclocerthia ruficauda*† | Rain forest | AF140899–AF140921 |
| *Contopus latirostris* | Rain forest | AY115201–AY115207 |
| *Cichlherminia lherminieri* | Rain forest | AY115158–AY115162 |
| *Cyanophaia bicolor* | Rain forest | AY115163–AY115166 |
| *Dendroica plumbea* | Rain forest | AF018226–AF018252 |
| *Eulampis jugularis* | Rain forest | AY082552–AY082563 |
| *Geotrygon montana* | Rain forest | AY082574–AY082583 |
| *Icterus dominicensis*‡ | Rain forest | AF109412–AF109423 |
| *Myadestes genibarbis* | Rain forest | AY115150–AY115157 |
| *Myiarchus oberi* | Rain forest | AY115173–AY115180 |
| *Troglodytes aedon* | Rain forest | AY115227–AY115237 |
| *Tangara cucullata* | Rain forest | AY115221–AY115224 |
| *Turdus fumigatus* | Rain forest | AY115238–AY115243 |

*Same as *Sericotes holosericeus.*

†Includes both *Cinclocerthia ruficauda* and *C. guttaralis.*

‡Includes all species in the *Icterus dominicensis* species complex: *I. dominicensis*, *I. laudabilis*, *I. bonana* and *I. oberi.*

### Species–area curves

I obtained the area of dry forest and rain forest on each island from Ricklefs & Lovette (1999). Combining this information with habitat-specific species lists for islands allowed me to construct separate species–area curves for dry forest and rain forest communities (*sensu* Buckley, 1982). Species–area curves were constructed based on habitat area (on each island) instead of island area. Two islands (St Eustatius and Saba) have less rain forest than the smallest amount of dry forest present on any island (9 km$^2$). Because species–area curves are best compared when they cover a similar range of areas (Diamond & Mayr, 1976; Connor & McCoy, 1979), I conducted analyses both excluding and including these islands. I used a linear regression of $\log_{10}$(species diversity) on $\log_{10}$(habitat area) to estimate the *z*-values of species–area curves. This is the approach that has traditionally been taken to estimate *z*-values (Rosenzweig, 1995) and thus allows comparison with the extensive species–area literature. I assessed how rain forest and dry forest species–area curves may differ by examining overlap in the 95% confidence intervals (CI) for estimates of the slope (*z*-value) and intercept parameters from these regressions. Additionally, I used a generalized linear model (GLM) framework to estimate and compare slope and intercept values, with $\log_{10}$(habitat area) as the independent variable, species diversity as the dependent variable, a Poisson error structure and a log-link. This is similar to the linear regressions above, but the Poisson error structure better accounts for the discrete count nature of the species diversity data. These analyses were conducted in the R Statistical Environment (R Development Core Team, 2007).

## Distance–decay analyses

I calculated the similarity in species composition of rain forest and dry forest communities on different islands using the Sørensen similarity index. There is only one rain forest species on Barbados and St Maarten, and these islands were therefore excluded from community similarity analyses. I assessed the effect of geographic distance on similarity of communities using a Mantel test, separately for dry forest and rain forest communities. I then determined if the rate of distance–decay (measured as the slope of the linear regression of community similarity on geographic distance) differs significantly between dry forest and rain forest communities. A permutation approach was taken because the community similarity measurements (the dependent variable) are not independent; each community is used in multiple similarity measurements. In order to generate a null expectation for the difference in rate of distance–decay, I randomly swapped the geographic coordinates of the islands 1000 times while maintaining the bird communities associated with each island (i.e. the existing locations were randomized among each other, and no new geographic locations were created). The proportion of the 1000 randomizations that had a difference in the rate of distance–decay between the null dry forest and rain forest communities greater than that found in the real data gave a *P*-value for this one-tailed test. I also assessed if the intercepts of the distance–decay relationship were significantly different using this approach. Distance–decay analyses were repeated using log-transformed community similarity values and geographic distances. This and all subsequent permutation analyses were conducted in the R Statistical Environment (R Development Core Team, 2007).

## Estimating dispersal between islands

I assessed the frequency of dispersal between islands for individual bird species using the mitochondrial DNA sequence data. I focused on measuring inter-island dispersal as opposed to dispersal between the mainland and the islands, because the former is likely to be more important in determining the species composition of individual islands. Nearly three-quarters of the Lesser Antillean avifauna is endemic (Terborgh *et al.*, 1978) and most non-endemic species have a deeper divergence with their colonization source than between island populations (Ricklefs, 2000; Ricklefs & Bermingham, 2007).

I first attempt to quantify dispersal by estimating *M*, the absolute number of migrants (successful dispersers) per generation between populations (Slatkin & Voelm, 1991). This is in contrast to estimating *m*, the proportion of individuals per generation that represent immigrants ($M = N_e m$). Obtaining an estimate of *m* requires estimating effective population size, $N_e$, and sample sizes are lacking in this study to accurately estimate $N_e$ for individual island populations. Regardless, it may be the absolute number of migrants per generation that is most significant in affecting macroecological patterns. For example, recolonization of islands after local extinction may be more probable with a greater numbers of migrants, and rescue-effects (Brown & Kodric-Brown, 1977), which would prevent the extinction of individual island populations, would be enhanced with greater total numbers of immigrants.

I used ARLEQUIN v.2.000 (Schneider *et al.*, 2000) to obtain an estimate of *M* between each pair of island populations for each species. *M* was calculated from $F_{ST}$ using the following formula: $M = (1-F_{ST})/2F_{ST}$. Some estimates of *M* were considered unrealistically high, particularly in cases where a single identical sequence is present in both populations ($F_{ST}$ is estimated as 0 and *M* is calculated as infinity). Thus, before subsequent analyses utilizing *M* estimates, I reset *M* estimates above a certain threshold value to the value of the threshold (e.g. if the threshold value is 20, then an estimate of 500 would be changed to 20). Analyses were conducted using two different thresholds: 20 and 5000. The former value was chosen as a reasonable cap while the latter value is higher than the highest non-infinity inter-island estimate of *M* (4253 migrants/generation) and thus only affects estimates of infinity. I then $\log_{10}$-transformed all *M* estimates (following Slatkin, 1993). For each species, I averaged the $\log_{10}(M)$ values obtained across all island pairs (so that each species is represented only once in the analysis) and compared dry forest and rain forest species for average $\log_{10}(M)$ using a Mann–Whitney *U*-test.

Most species were not sampled from enough islands to allow for a formal isolation by distance analysis (Slatkin, 1993). I therefore grouped all pairwise comparisons for all species by habitat to determine if the general relationship between $\log_{10}$(geographic distance) and $\log_{10}(M)$ differs for rain forest and dry forest species. Specifically, I used a permutation approach to assess if the slope of the relationship between $\log_{10}$(geographic distance) and $\log_{10}(M)$ differs for species in the two habitats significantly more than expected by chance. I combined all pairwise estimates of $\log_{10}(M)$ and $\log_{10}$(geographic distance) for all species into a common pool. I then randomly drew, without replacement, eight species and their respective $\log_{10}(M)$ and $\log_{10}$(geographic distance) values to represent null dry forest communities, while the remaining 13 species in the pool represented the null rain forest communities (the original data have information for eight dry forest and 13 rain forest species). I repeated this 1000 times and determined the proportion of replicates that have a difference in slope between rain forest and dry forest species greater than that in the real data, which gives a $P$-value for this statistical test. As above, this approach was taken because the migration estimates (the dependent variable) are not independent, each island population being used for multiple migration estimates. I conducted this analysis both excluding $M$ estimates of infinity and restricting maximum $M$ values to 20 and 5000 as above.

### An alternative approach to estimating inter-island dispersal

If two island populations form distinct genetic clusters (i.e. if they are reciprocally monophyletic with respect to each other), then the estimate of $M$ based on $F_{ST}$ will effectively be zero, regardless of the amount of genetic divergence between the two populations. However, the genetic divergence between island populations is related to the time since the last effective dispersal event between those islands, either directly or via another island. Analyses of $M$ ignore the information about dispersal present in the depth of inter-island divergences, which could inform comparisons of dispersal between rain forest and dry forest communities. In order to take advantage of this information, I devised an alternative approach to compare dispersal rates between dry forest and rain forest communities based on sequence divergence between island populations.

I obtained the Nei & Li (1979) genetic distance, $D_A$, between all pairs of island populations for each species using the Tamura and Nei distance formula in Arlequin v.2.000 (Schneider *et al.*, 2000). I combined all inter-island estimates of $D_A$ for all species by habitat, giving a separate distribution of $D_A$ estimates for dry forest and rain forest communities. I assume that the rate of dispersal between islands is constant through time for all species within a given habitat and that the per island extinction rate is constant through time for all species across both habitats. While one study has suggested temporal heterogeneity in these rates (Ricklefs & Bermingham, 2001), the data are also consistent with rate constancy (Cherry *et al.*, 2002; Ricklefs & Bermingham, 2004b). I also assume that a dispersal event between two islands resets $D_A$ to zero. Given these assumptions, the distribution of $D_A$ estimates should be exponential with a rate parameter that approximates the average rate of inter-dispersal across species within a given habitat.

I next assessed whether the distributions of $D_A$ estimates are significantly different for dry forest and rain forest communities. Because each island population is used in multiple pairwise comparisons and $D_A$ estimates are not independent, I used a permutation-based approach to generate a null expectation for how different the $D_A$ distributions could be by chance. I combined the $D_A$ estimates for all species from dry forest and rain forest into one pool and then randomly drew species (and their associated $D_A$ values) without replacement for the null communities (eight species for dry forest and 13 for rain forest). I then obtained the likelihood ratio that the $D_A$ estimates from the two null communities belong to two different exponential distributions instead of one. I performed this permutation 1000 times and assembled a null distribution of likelihood ratios. I determined the proportion of the null distribution that has a likelihood ratio greater than that in the original data, which gives a $P$-value for this one-tailed test. I repeated this analysis using only $D_A$ estimates between neighbouring islands.

## RESULTS

### Distribution analyses

Rain forest species occupy a lower proportion of islands with suitable habitat than dry forest species (rain forest: 0.28 ± 0.06 SE; dry forest: 0.60 ± 0.08 SE; Mann–Whitney $U$-test, $P = 0.0147$). Additionally, the number of unoccupied islands with suitable habitat that are adjacent to occupied islands is greater for rain forest than dry forest species (rain forest: 2.1 islands ± 0.2 SE; 1.2 islands ± 0.3 SE; Mann–Whitney $U$-test, $P = 0.0160$).

### Species–area curves

Both rain forest communities and dry forest communities show a significant species–area relationship (Fig. 1; rain forest $F = 32.2$, $P = 0.0003$; dry forest $F = 8.8$, $P = 0.0104$). However, these species–area relationships differ significantly in both slope [rain forest 0.42 (95% CI 0.27, 0.57); dry forest 0.09 (95% CI 0.02, 0.14)] and intercept [rain forest −0.05 (95% CI −0.38, 0.28); dry forest 0.85 (95% CI 0.72, 0.98)], as indicated by the lack of overlap in the 95% CIs ($P < 0.05$). This result holds when rain forest communities with < 9 km$^2$ of rain forest are included in the analysis [slope 0.34 (95% CI 0.16,

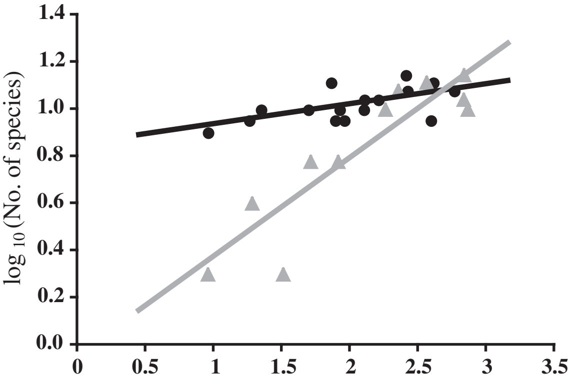

**Figure 1** The species–area relationship for dry forest communities (black circles, $n = 16$) and rain forest communities (grey triangles, $n = 13$) of birds in the Lesser Antilles. The lines represent the best-fit least squares linear regression of $\log_{10}$(no. species) on $\log_{10}$(area of habitat) for dry forest ($y = 0.09x + 0.85$) and rain forest ($y = 0.42x–0.05$). These species–area curves are significantly different (see Results: Species–area curves).

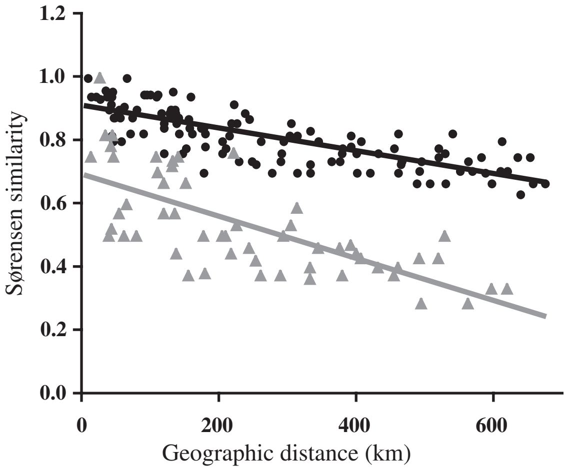

**Figure 2** Distance–decay in the similarity in species composition between dry forest (black circles, $n = 120$ comparisons) and rain forest communities (grey triangles, $n = 55$ comparisons) of birds in the Lesser Antilles. The lines represent the best-fit least squares linear regression of Sørensen similarity on geographic distance for dry forest ($y = -0.0004x + 0.91$) and rain forest ($y = -0.0007x + 0.69$). The significance of relationships was assessed using a Mantel test (see Results: Distance–decay analyses).

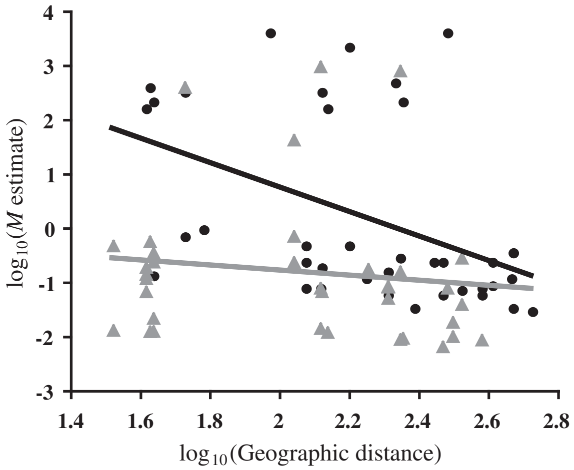

**Figure 3** Isolation by distance patterns for Lesser Antillean bird species in dry forest (black circles, $n = 38$ comparisons) and rain forest (grey triangles, $n = 36$ comparisons). The lines represent the best-fit least squares linear regression of $\log_{10}(M)$, the number of migrants per generation, on $\log_{10}$(geographic distance) for dry forest ($y = -2.26x + 5.28$) and rain forest ($y = -0.47x + 0.16$).

0.53); intercept 0.06 (95% CI −0.32, 0.43)]. When a Poisson error structure (with a log-link) is used in regressions under a GLM framework, a lack of overlap in the 95% CIs is also observed for both the slope [rain forest 0.98 (95% CI 0.57, 1.43); dry forest 0.22 (95% CI −0.10, 0.55)] and intercept parameter estimates [rain forest −0.26 (95% CI −1.40, 0.74); dry forest 1.82 (95% CI 1.10, 2.49)].

### Distance–decay analyses

In both rain forest and dry forest communities, similarity in community composition is negatively correlated with geographic distance (Fig. 2; Mantel test, rain forest $r = 0.71$, $P < 0.001$; dry forest $r = 0.79$, $P < 0.001$). However, proximate rain forest communities are less similar on average (i.e. they have a lower $y$-intercept; permutation test, $P = 0.002$) and decline more in similarity with distance (permutation test for slope, $P = 0.01$). Distance–decay analyses using log-transformed similarity values and geographic distances gave equivalent results and are not presented here.

### Assessment of dispersal between islands

There is a complex relationship between geographic distance and migration rate (Fig. 3). There appear to be pairs of islands that exchange many migrants while most islands exchange few migrants, regardless of geographic distance. Nevertheless, some patterns do emerge. At large distances (> 250 km), populations of both dry forest and rain forest species exchange few migrants, while at close distances (< 65 km) dry forest populations exchange more migrants on average. The permutation test shows that the relationship between geographic distance and migration rate differs significantly for rain forest and dry forest species when $M$ estimates of infinity are excluded (Fig. 3, $P = 0.013$), although this difference is not statistically significant when the maximum $M$ value is set to 20 ($P = 0.207$) or 5000 ($P = 0.129$). When ignoring geographic distance, the species-level average $\log_{10}(M)$ estimates were significantly lower for rain forest than dry forest, whether the maximum $M$ value is set to 20 [mean difference on $\log_{10}$ scale (raw scale): 1.3 (6) migrants/generation; Mann–Whitney $U$-test, $P = 0.0022$] or 5000 [mean difference on $\log_{10}$ scale (raw scale): 2.7 (359) migrants/generation; Mann–Whitney $U$-test, $P = 0.0018$].

Dry forest and rain forest communities have significantly different distributions of inter-island genetic distances (permutation test, $P = 0.008$), which is evident in Fig. 4. While

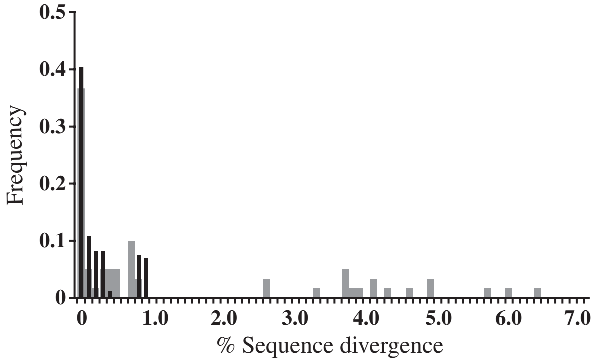

**Figure 4** Relative frequency of inter-island genetic distances, $D_A$, for dry forest (black bars, foreground) and rain forest species (grey bars, background). Nei and Li genetic distances were calculated using the Tamura and Nei distance formula in Arlequin v.2.000 and are given as percentage sequence divergence (Schneider *et al.*, 2000).

the largest class for both communities is zero genetic distance, the tail of the exponential distribution in rain forest communities includes many more deep divergences than dry forest communities. The significant difference in distributions persists if analyses are restricted to populations on neighbouring islands ($P = 0.015$).

## DISCUSSION

Differences in dispersal ability are often assumed to underlie contrasting macroecological patterns, but this is rarely tested. Here, I show how population genetic data can be used to assess dispersal ability and test if dispersal plays a role in shaping macroecological patterns. Significantly, these population genetic data are derived independently from data, such as species lists or distribution maps, used to elucidate macroecological patterns.

In the Lesser Antilles, rain forest and dry forest bird communities show contrasting macroecological patterns that would be expected if dry forest species disperse between islands more often than rain forest species. Dry forest species are found on nearly all islands, which gives a nearly flat species–area curve with a high intercept, while rain forest species are more limited in distribution and show a steep species–area relationship (Fig. 1). Dry forest communities also show shallower distance–decay in community similarity than rain forest communities (Fig. 2). In fact, it is the combination of the distance–decay and species–area patterns in particular that suggest that dry forest species are less dispersal limited (Hovestadt & Poethke, 2005). Population genetic analyses show that dry forest species do indeed disperse between islands more frequently than rain forest species (Figs 3 & 4). This illustrates that dispersal is a significant drive of macroecological patterns in the Lesser Antilles. This explanation differs from, but is potentially complementary to, previous explanations, such as the taxon cycle (Ricklefs & Cox, 1978; Ricklefs & Bermingham, 1999, 2002), that primarily emphasize the role of history and extinction. These alternative explanations are discussed below, along with interpretations of the population genetic data.

### Interpretation of dispersal analyses

Analyses of estimates of $M$ suggest that dry forest birds have higher average rates of dispersal among communities than rain forest birds. This difference is most notable among proximate islands (Fig. 3). Dispersal between neighbouring islands is likely to be critical in influencing distribution patterns of Lesser Antillean birds, as dispersal across the archipelago is thought to occur in a stepping-stone fashion (Ricklefs & Bermingham, 2001, 2004a). If rain forest species are more limited in dispersal between neighbouring islands, this can help explain why they have patchy and limited distributions. Furthermore, proximate rain forest communities are less similar in species composition than proximate dry forest communities are (Fig. 2), which is also commensurate with differences in dispersal between neighbouring islands.

The distributions of inter-island genetic divergences were significantly different between the two habitats, with many, deeper, divergences in rain forest (Fig. 4). Assuming that dispersal and extinction rates have been constant through time, the rate parameter from this exponential distribution should approximate the rate of dispersal between islands, and this rate parameter is lower in the rain forest. The metric used to measure divergence, $D_A$, can also depend on $N_e$, the effective population size. It is not known if $N_e$ differs systematically between populations of dry forest and rain forest species, and population genetic sample sizes are too small to estimate $N_e$. For now, it can be stated that the results from analyses of $D_A$ are in accord with analyses of $M$ in suggesting that rain forest species disperse between islands less frequently than dry forest species.

There are many reasons why rain forest species might disperse between islands less often than dry forest species. Dry forest scrub is a relatively open habitat compared to rain forest, and bird species are more reluctant to cross an area the more different it is in structural characteristics from their preferred habitat (Antongiovanni & Metzger, 2005). Rain forest birds may be averse to crossing open water because of increased susceptibility to predation or because of an intolerance of bright, direct sunlight (Johns, 1992). Additionally, some rain forest species may be physically incapable of flying more than a few hundred metres without landing (Moore *et al.*, 2008). Finally, rain forest species may be 'psychologically flightless', meaning that they are actually psychologically incapable of crossing open water (Diamond, 1981). Mainland studies have also shown that rain forest birds are less likely to cross open spaces (e.g. roads, agricultural landscapes) than are dry forest or scrub species, presumably for the same reasons (Laurance *et al.*, 2004; Sodhi *et al.*, 2004; Antongiovanni & Metzger, 2005).

Alternatively, if hurricanes or other storms carry birds between islands in the Lesser Antilles, it might be expected that dry forest species, which occur in a peripheral, low-elevation habitat, are more frequently dispersed via this passive mechanism (Terborgh & Faaborg, 1980).

The results from population genetic analyses could stem from processes other than dispersal. For example, estimates of genetic differentiation between island populations can reflect differential selection among island populations. However, nearly all the substitutions recorded in dry and rain forest species are synonymous and are thus unlikely to be affected by selection. Alternatively, given that the mitochondrion is maternally inherited in birds, an interaction between habitat type and sex-biased dispersal (e.g. different breeding systems in different habitats) could explain the results. However, there is no a priori reason to expect such an interaction. The same guilds and families of birds, which often share the same breeding systems, are present in each habitat and show similar ecological and genetic patterns (K.G.D., unpublished data).

Another issue that must be addressed in this study is that I am measuring effective dispersal, which is a combination of successful dispersal and successful establishment. It may be that rain forest species do disperse between islands as frequently as dry forest species, but that it is more difficult for individuals of rain forest species to establish successfully. However, establishment limitation on its own will not lead to distance–decay in community similarity, which is observed in both communities. This indicates that dispersal limitation is likely to be more important than establishment limitation in driving the macroecological patterns observed in this system (Hovestadt & Poethke, 2005).

Finally, the sample sizes used to estimate inter-island dispersal in this study are low, often only two individuals per island. Estimates of $F_{\mathrm{ST}}$ and $D_{\mathrm{A}}$ can be obtained with such low sample sizes, although they are prone to error. However, this error should not bias results differently for dry forest and rain forest species and should only serve to erase the statistical signal of any difference between them. Hence, it is all the more remarkable that the analyses do show statistically significant differences in these parameters between rain forest and dry forest species. Even when sample sizes are small, population genetic data can be useful for assessing if dispersal shapes macroecological patterns.

## Alternative explanations for contrasting macroecological patterns

The distribution of relative abundances of species, the spatial aggregation of individuals within species and sampling effects can all affect the form of macroecological patterns (He & Legendre, 2002; Plotkin & Muller-Landau, 2002; Woodcock *et al.*, 2006; Morlon *et al.*, 2008). This study includes no data on relative abundances or individuals' aggregation, and thus I cannot quantify the effect of these factors per se on the observed macroecological patterns. However, the influence of these factors is generally felt through their interaction with sampling, and sampling effects are unlikely to be very significant in this study. Hundreds of amateur bird watchers, plus many professionals, visit the Lesser Antilles every year, covering all habitat types on nearly every island. Rare species are especially sought out, and these repeated surveys have probably led to the documentation of nearly all, if not all, resident species in dry forest and rain forest on each island.

The spatial position of islands and distance to mainland colonization sources can affect both the slope of the species–area curve and the rate of distance–decay in communities (MacArthur & Wilson, 1967; Diamond & Mayr, 1976; Nekola & White, 1999). However, I have controlled for the effects of geography in this study by contrasting communities found in the same archipelago and on the same individual islands.

Environmental heterogeneity also has the potential to shape macroecological patterns. Larger areas may contain more species than small islands because they contain greater environmental heterogeneity, not because they are at different immigration–extinction equilibria (Terborgh & Faaborg, 1980; Rosenzweig, 1995). If environmental heterogeneity scales with area to a greater degree in rain forest than in dry forest, this could explain why rain forest communities have a steeper species–area curve. However, bird species in the Lesser Antilles are not generally limited in their distribution to specific subhabitats within rain forest or dry forest and instead occur across the breadth of environmental variation found within either habitat (Ricklefs & Cox, 1978; Terborgh & Faaborg, 1980; Faaborg, 1985). Similarly, distance–decay may be caused not by limited dispersal but by environmental gradients and species responding in their distribution to these environmental gradients (Nekola & White, 1999). If there are important environmental gradients, within rain forest and dry forest, across the Lesser Antilles and environmental gradients in rain forest are steeper, then this could explain the steeper distance–decay in rain forest communities. However, several authors have emphasized that neither rain forest nor dry forest change greatly in their habitat characteristics across the archipelago (Ricklefs & Cox, 1978; Terborgh & Faaborg, 1980; Ricklefs & Lovette, 1999). Thus, previous studies of Lesser Antillean bird communities suggest that environmental heterogeneity may not be an important factor driving macroecological patterns in this system.

As discussed above (see Introduction), Ricklefs and colleagues (Ricklefs & Cox, 1972, 1978; Ricklefs & Bermingham, 1999, 2004a) have explained contrasting macroecological patterns in Lesser Antillean birds as part of the taxon cycle hypothesis. The low inter-island genetic divergence observed for dry forest species (Fig. 4) could be due to recent colonization, as predicted by the taxon cycle hypothesis, rather than frequent inter-island dispersal over time, as hypothesized in this study. Ideally, the relative influence of colonization time and subsequent dispersal on the population genetic patterns could be determined (*sensu* Nielsen & Wakeley, 2001; Hey & Nielsen, 2007), but this requires much larger sample sizes. However, the taxon cycle hypothesis also predicts no recent inter-island movement for rain forest species, while the genetic data clearly show that many rain forest species have recently moved between islands. The largest class of inter-island divergences for rain forest species, as for dry forest species, is zero (Fig. 4). Even so, rain forest species seem to disperse less frequently between islands, which is evidenced by the long tail of deep divergences in Fig. 4 as well as in analyses of $M$ (Fig. 3). Thus, the dispersal limitation hypothesis outlined here may agree better with some aspects of the population genetic data. In addition, the taxon cycle hypothesis does not necessarily predict the observed distance–decay in community similarity, while the dispersal limitation hypothesis does.

If the taxon cycle is extended to include multiple cycles of extinction and distance-dependent colonization (Ricklefs & Cox, 1972, 1978; Ricklefs & Bermingham, 1999, 2002, 2004a), then it could also explain the observed differences in the distance–decay and species–area relationships between dry forest and rain forest birds. Distinctions between this extended version of the taxon cycle hypothesis and the dispersal hypothesis outlined here are of degree, and both the taxon cycle and post-colonization inter-island dispersal are likely to shape distribution patterns of Lesser Antillean birds.

Pleistocene climate cycles may have also played a role in shaping distribution patterns of Lesser Antillean birds. During glaciation phases, sea levels were lower, exposing more land that was presumably covered in dry forest scrub (Pregill & Olsen, 1981). Many of the islands that currently have a small area of dry forest may have had much larger areas of dry forest in the past, particularly during the Last Glacial Maximum. Dry forest communities on these islands may not have responded yet, in terms of island population extinctions, to the current reduction in area. Furthermore, the greater land exposed means that dry forest patches on individual islands may have been closer to each other, which would have facilitated dispersal between islands for dry forest species. Finally, during glaciation phases, the climate was probably drier, and rain forests may have contracted in size, perhaps disappearing from smaller islands (Pregill & Olsen, 1981). All of these factors could have contributed to the current pattern that most dry forest species are found on most islands, while rain forest species have patchier distributions, principally being found on larger islands. Thus, climate fluctuations in the Pleistocene provide an alternative explanation for the macroecological patterns of Lesser Antillean birds. Further palaeoecological research is needed to address this possibility (*sensu* Reis & Steadman, 1999).

## CONCLUSIONS

Rain forest communities have a steeper species–area curve than dry forest communities and greater distance–decay in community similarity. Both conventional analyses of $M$, the number of migrants per generation between island populations, and alternative analyses of $D_A$, the genetic distance between island populations, suggest that rain forest species disperse between islands less frequently than dry forest species. Thus, reduced dispersal of rain forest species is a plausible explanation for these contrasting macroecological patterns. Historical factors, such as the taxon cycle and Pleistocene climate cycles, probably also played a role in establishing current distribution patterns of Lesser Antillean birds. Further population genetic data are needed to definitively clarify the relative importance of these various processes. Nevertheless, this paper has shown how population genetic data can be used to test macroecological theories, and that dispersal is likely to be an important process in shaping macroecological patterns of Lesser Antillean birds.

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## BIOSKETCH

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