MOLECULAR ECOLOGY

Molecular Ecology (2011) **20**, 5012–5024 doi: 10.1111/j.1365-294X.2011.05073.x

Ancient islands and modern invasions: disparate phylogeographic histories among Hispaniola's endemic birds

NICHOLAS D. SLY,* ANDREA K. TOWNSEND,* CHRISTOPHER C. RIMMER,† JASON M. TOWNSEND,‡ STEVEN C. LATTA§ and IRBY J. LOVETTE*

**Fuller Evolutionary Biology Program, Cornell Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA, †Vermont Center for Ecostudies, PO Box 420, Norwich, VT 05055, USA, ‡College of Environmental Science and Forestry, State University of New York, 1 Forestry Drive, Syracuse, NY 13210, USA, §National Aviary, Allegheny Commons West, 700 Arch Street, Pittsburgh, PA 15212, USA*

Abstract

With its large size, complex topography and high number of avian endemics, Hispaniola appears to be a likely candidate for the *in situ* speciation of its avifauna, despite the worldwide rarity of avian speciation within single islands. We used multilocus comparative phylogeography techniques to examine the pattern and history of divergence in 11 endemic birds representing potential within-island speciation events. Haplotype and allele networks from mitochondrial ND2 and nuclear intron loci reveal a consistent pattern: phylogeographic divergence within or between closely related species is correlated with the likely distribution of ancient sea barriers that once divided Hispaniola into several smaller paleo-islands. Coalescent and mitochondrial clock dating of divergences indicate species-specific response to different geological events over the wide span of the island's history. We found no evidence that ecological or topographical complexity generated diversity, either by creating open niches or by restricting long-term gene flow. Thus, no true within-island speciation appears to have occurred among the species sampled on Hispaniola. Divergence events predating the merging of Hispaniola's paleo-island blocks cannot be considered *in situ* divergence, and postmerging divergence in response to episodic island segmentation by marine flooding probably represents *in situ* vicariance or interarchipelago speciation by dispersal. Our work highlights the necessity of considering island geologic history while investigating the speciation–area relationship in birds and other taxa.

Keywords: Hispaniola, island, phylogeography, speciation

Received 28 November 2010; revision received 10 February 2011; accepted 17 February 2011

Introduction

Island endemic speciation can occur either through anagenesis of an immigrant population or by divergence of populations within islands. The probability of *in situ* speciation, and its relative contribution to island diversity, is predicted to increase with factors such as island size, ecological diversity, island age and isolation from source populations (Diamond 1977; Losos & Schluter 2000; Lomolino 2000; Parent & Crespi 2006; Gillespie & Baldwin 2010; Losos & Parent 2010). Larger islands provide more opportunities for divergence, but only above a threshold minimum island size necessary for *in situ* speciation to occur, determined by levels of dispersal and gene flow connecting populations (Diamond 1977; Losos & Schluter 2000; Lomolino 2000; Kisel & Barraclough 2010). Although quantitative examinations of this speciation–area relationship have been few, a speciation–area relationship and a minimum island size requirement for *in situ* speciation have been described in Caribbean *Anolis* lizards (Losos & Schluter 2000) and

Correspondence: Nicholas D. Sly, Fax: 607 254 2486;
E-mail: nds22@cornell.edu

a range of plant and animal taxa (Kisel & Barraclough 2010).

Diamond (1977) predicted that only the largest islands (i.e. Madagascar and New Guinea, *c.* 500 000+ km^2) could support within-island avian speciation, because of the inferred high dispersal capabilities of birds. There is little evidence for avian speciation on most smaller islands, although several studies have documented a minimum island size for *in situ* avian speciation orders of magnitude lower than Diamond's (Coyne & Price 2000; Kisel & Barraclough 2010). The smallest within-island avian divergences have been documented in the Tristan da Cunha archipelago (Inaccessible Island, 14 km^2; Ryan *et al.* 2007) and Reunion (2512 km^2; Mila *et al.* 2010). Jamaica (10 900 km^2) is the next smallest island with concrete evidence for *in situ* avian speciation (Gill *et al.* 1973; Coyne & Price 2000; Kisel & Barraclough 2010), suggesting that birds can speciate within a much smaller landmass than predicted by Diamond (1977) and that they are sometimes more susceptible to restricted gene flow than expected given their volant nature.

Understanding the role of area in avian island speciation will require more investigation of the processes underlying within-island divergence. Phylogeographic studies have been used to investigate the origins of within-island divergence by temporally and spatially identifying barriers to gene flow that led to vicariance. Although some phylogeographic studies have correlated divergence to within-island barriers such as volcanic flows (Brown *et al.* 2006; Mila *et al.* 2010), others have correlated species divergences on islands with prehistoric marine barriers (Gifford *et al.* 2004; Glor *et al.* 2004; Townsend *et al.* 2007; Gifford & Larson 2008; Sly *et al.* 2010). In these cases, it is the idiosyncratic nature of island history, rather than such factors as island size or ecological diversity, driving apparent *in situ* divergence.

Hispaniola is a large Caribbean island (*c.* 76 000 km^2) with high endemic diversity, including four closely related avian taxon pairs that have been recognized as potentially arising from within-island speciation events (Keith *et al.* 2003): two palm-tanagers in the endemic genus *Phaenicophilus*, two chat-tanagers in the endemic genus *Calyptophilus*, two todies (*Todus*), and two ground-warblers in monotypic endemic genera, *Microligea palustris* and *Xenoligea montana*. The members of one taxon pair, the Narrow-billed and Broad-billed Todies (*Todus angustirostris* and *T. subulatus*, respectively), are not sister species and thus probably represent a double invasion of the island (Ricklefs & Bermingham 1997; Overton & Rhoads 2004). Two of the taxon pairs, the two palm-tanagers (*Phaenicophilus*) and the two ground-warblers (*Microligea* and *Xenoligea*), have been shown to form a monophyletic group (Klein *et al.* 2004), thus providing evidence for a single-island radiation of four species. Hispaniola is much smaller than Diamond's (1977) predicted minimum island size for avian *in situ* speciation. However, it is much larger than the smallest islands with potential *in situ* speciation events in Kisel & Barraclough (2010). The multiple taxon pairs of Hispaniola, each with different ranges and ecological requirements (e.g., highland vs. generalist, widespread vs. restricted across the island; Keith *et al.* 2003), provide a robust opportunity for a comparative look at divergence processes within an island.

The objective of this paper is to examine the relative impact of ecological, geologic and historical processes on the diversification of Hispaniola's endemic avifauna. Using multilocus phylogeographic methods, we correlate divergence patterns within and between species to current and historical barriers to gene flow. We compare the phylogeographic patterns found within the four endemic taxon pairs and further examine three additional endemic species or subspecies (*Spindalis dominicensis, Myadestes genibarbis montanus* and *Elaenia fallax cherriei*) that are part of more widespread Caribbean radiations. We hypothesize that these subspecies colonized Hispaniola after the major geologic events and will not have been affected by them. The eleven species analysed represent a mix of montane specialists and lowland generalist species, allowing an examination of the effects of ecology on the divergence patterns observed. If Diamond's (1977) hypothesized island size requirement for avian speciation is correct, then the divergence patterns detected within and between species should correlate spatially and temporally with the ancient water barriers, rather than with contemporary ecological and topographical barriers.

Materials and methods

Geologic history of Hispaniola and potential barriers to gene flow

Present-day Hispaniola originated as two distinct island blocks (hereafter referred to as the North and South paleo-island) that merged in the mid-Miocene [*c.* 8 million years ago (Ma)] along a border represented now as the low-lying Cul-de-Sac Plain (Graham 2003). This east–west running valley is largely below sea level, contains multiple saline lakes and has been repeatedly flooded by high sea levels, maintaining a saltwater barrier between the North and South paleo-islands as recently as the late Pleistocene interglacials (McLaughlin *et al.* 1991; Mann *et al.* 1991). A second major water barrier, a sea channel that split the Tiburon Peninsula of southwestern Haiti from the rest of the South paleo-island block, only disappeared via uplift as recently as

100 000 years ago (Maurrasse *et al.* 1982). The present-day topography of the island consists of several high mountain ridges running parallel east–west, separated by lowland valleys that formed 8–20 Ma and have been largely stable since (Heubeck & Mann 1991). This complex topography provides high ecological diversity that has resulted in adaptive within-island radiations in some nonavian taxa (Glor *et al.* 2003; Losos & Parent 2010). These barriers to dispersal have all been implicated in taxon divergences of varying ages, and each separated region supports unique endemic populations (lizards: Glor *et al.* 2003; Gifford *et al.* 2004; Gifford & Larson 2008; birds: *Todus angustirostris*—Ricklefs & Bermingham 1997; Overton & Rhoads 2004; *Calyptophilus*—Townsend *et al.* 2007; *Phaenicophilus*—Sly *et al.* 2010). Given the differing ranges and ecological requirements in each of the endemic avian taxon pairs (Keith *et al.* 2003), they may differ in the dispersal barriers that led to the divergence of each pair.

Laboratory and analysis methods

Samples were obtained from 2002 to 2006 during island-wide surveys of avian diversity; locations and sample sizes for each species are summarized in Fig. 1 and Table 1. The individuals sampled were not vouchered as specimens because they were captured during ongoing mark–recapture studies of survivorship and other demographic variables (Latta *et al.* 2003; Rimmer *et al.* 2003, 2005; Townsend & Rimmer 2006). We took approximately 80 μL of blood from each individual with heparinized capillary tubes via brachial venipuncture with sterile 27-gauge hypodermic needles. Blood samples were stored in 0.5 mL blood lysis buffer [100 mM Tris–HCl, pH 8; 100 mM Na_2 EDTA; 10 mM NaCl; 0.5% SDS; White & Densmore 1992].

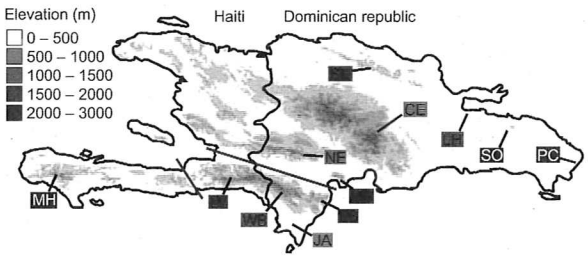

Fig. 1 Sampling locations and topography on Hispaniola. Grey shading indicates elevation in metres. The blue line indicates the low-elevation valley at the divide between the North and South paleo-island blocks that merged in the Miocene (8 Ma). The red line indicates the location of a sea channel separating the Tiburon Peninsula from the South paleo-island block as recently as 100 000 years ago. Locality symbols correspond to those in Table 1. Locality colours correspond to those in Figs 2–4.

We extracted DNA from each sample using Perfect gDNA Blood Mini kits (Eppendorf) following the manufacturer's protocol. We amplified and sequenced one mitochondrial gene and several nuclear introns per taxon (Table 1) using the protocols of Lovette & Rubenstein (2007) and the following primers: mitochondrially encoded NADH dehydrogenase subunit 2 (ND2) with primers METb and TRPc (Eberhard & Bermingham 2004), beta-fibrinogen intron 5 (Fib-5) with primers Fib-5 and Fib-6 (Lovette & Rubenstein 2007), and Z-linked aconitase-1 intron 9 (Aco-9) with primers AcoI10F and AcoI10R2 (Barker *et al.* 2008).

ND2 sequenced poorly in the *Todus* species, resulting in a reduced data set at this locus for *T. angustirostris* (Table 1) and no ND2 data for *T. subulatus*. A small number of *T. angustirostris* samples were cloned using the pGEM-T Easy TA cloning kit (Promega, Madison, WI, USA) and compared with the PCR-amplified sequences. PCR-amplified and cloned sequences had nearly identical haplotypes in samples from both North and South paleo-islands. The absence of insertions, deletions, nucleotide polymorphisms and stop codons in the reading frame suggests that the ND2 sequences for *T. angustirostris* reported here are not nuclear pseudogenes (Sorenson & Quinn 1998).

Sequences were aligned by eye in Sequencher™ (Gene Codes). All individuals were sexed by PCR amplification of an intron of chromo-helicase DNA-binding protein with primers 2550F and 2718R (Fridolfsson & Ellegren 1999)—the Z and W chromosome copies of this locus differ in length and were scored by eye using gel electrophoresis. Heterozygous intron sequences were resolved as individual alleles using PHASE 2.1 (Stephens *et al.* 2001; Stephens & Scheet 2005) under default parameters and using the best pairs suggestions. Both alleles from each intron were included in analysis for every individual, except for the Z-linked Aco-9, for which females have only one allele. We chose the optimal model of sequence evolution for ND2 using the model selection analysis in TOPALi v2 (the top model selected by hierarchical likelihood ratio tests; Milne *et al.* 2009) and applied in PAUP* (Swofford 2000) to analyse corrected nucleotide variation. We constructed statistical parsimony haplotype networks using TCS 1.21 (Clement *et al.* 2000) to estimate relationships among haplotypes and alleles. Indels were coded as present or absent for these analyses.

We employed two methods for estimating divergence times for the major phylogeographic divergences detected within or between species—the mitochondrial clock alone and multilocus coalescent analyses of divergence time. For the first, we used the model-corrected divergence in ND2 between groups calculated in PAUP* (Swofford 2000) with a molecular rate of 2.1% (±0.1%,

Table 1 Sample sizes and loci sequenced for all species

			Location											
Species	Loci	Total *N*	MH	LV	WB	JA	EB	MG	NE	CE	SE	LH	SO	PC
*Calyptophilus frugivorous**	NAFM	20					3	1	5	11				
*Calyptophilus tertius**	NAFM	28	8	5	15									
Phaenicophilus palmarum†	NAFR	28		5	5	5		4		2	1	3		3
Phaenicophilus poliocephalus†	NAFR	9	9											
Microligea palustris	NAF	46		5	10	2		8	10	10		1		
Xenoligea montana	NAF	20	10		10									
Todus angustirostris	NAF	34	6 (2)	3 (3)	5 (0)		5 (1)	5 (1)	1 (1)	4 (2)	5 (2)			
Todus subulatus	AF	44	1		4	9		5		1	7	5	3	9
Myadestes genibarbis	N	24	5	3	4		5	1	1	5				
Spindalis dominicensis	N	24	5	2	2		5	5		5				
Elaenia fallax	N	16	1	1	4		1	3	2	4				

Numbers reported for *T. angustirostris* are for nuclear introns, with sample sizes for ND2 in parentheses. South paleo-island locations (shaded grey): MH, Massif de la Hotte (Tiburon Peninsula); LV, La Visite; WB, Western Sierra de Bahoruco; JA, Jaragua; EB, Eastern Sierra de Bahoruco. North paleo-island locations: MG, Sierra Martin Garcia; NE, Sierra de Nieba; CE, Cordillera Central; SE, Cordillera Septentrional; LH, Los Haitises; SO, Sierra Oriental; PC, Punta Cana. Loci: ND2 (N), Aco-9 (A), Fib-5 (F), Musk-4 (M), Rho-1 (R).

*From Townsend *et al.* (2007).

†From Sly *et al.* (2010).

95% confidence interval) divergence per million years, the average rate of divergence for the mitochondrial cytochrome B gene in birds (Weir & Schluter 2008).

Divergence estimates among the genera of the endemic clade (*Phaenicophilus*, *Microligea*, and *Xenoligea*) were exceptionally high (41.0–53.4%) using the optimal model (GTR + G with G = 0.272), exceeding likely values of divergence for the base of the nine-primaried oscine radiation (*c.* 25%, J. Weir, personal communiation). Including only a small number of taxa may lead to biased model parameter estimation (J. Weir, personal communiation), so we reran the model estimation in TOPALi using our data plus ND2 sequences from an array of 42 related species (Genbank accession numbers listed in Data S1, Supporting information). We reran the distance matrices with the new best model (GTR + G + I, g = 0.769, pINV = 0.382), but once again recovered unrealistically large distance estimates. We ran a Tamura–Nei model (the third most likely model based on AIC scores in TOPALi) with all substitutions and a gamma parameter of g = 0.769 in MEGA 4 (Tamura *et al.* 2007), which gives lower, more realistic divergence estimates and report those values in Table 2.

For the second estimate of divergence time, we used the isolation with migration-analytic (IMa) (Nielsen & Wakely 2001; Hey & Nielsen 2004, 2007) for multilocus coalescent analysis of divergence time and demographic parameters of the diverging populations. IMa requires selectively neutral, recombination-free, independent loci. We assumed the mitochondrial data to be recombination free and tested for recombination in all nuclear loci using the four-gamete test (Hudson & Kaplan 1985) in DnaSP 4.0 (Rozas *et al.* 2003). We selected the largest recombination-free segment with segregating sites for analysis and tested for neutrality in these using the Hudson–Kreitman–Aguade (HKA) test (Hudson *et al.* 1987) in DnaSP 4.0 (Rozas *et al.* 2003). We used the Hasegawa–Kishino–Yano model to fit our recombination-free segments to the IMa model and ran multiple preliminary metropolis coupled Monte Carlo Markov chain simulations of variable length to optimize parameter bounds and mixing. We ran three final simulations with a burn-in of $1*10^6$ steps, a geometric heat mode, thirty chains and different random seeds for each simulation, until parameter effective samples sizes reached at least 100. We converted the time parameter estimates (scaled to the neutral mutation rate) to demographic units (years since divergence) by calculating the geometric mean per locus mutation rate for each data set, using a molecular rate of 1.35×10^{-9} substitutions/site/year (s/s/y) for nuclear loci (the midpoint of the mean range, $1.2–1.5 \times 10^{-9}$ s/s/y, in Ellegren 2007) and a rate of 2.1×10^{-8} s/s/y for the mitochondrial locus (Weir & Schluter 2008).

For comparative purposes, we include the molecular data sets for *Calyptophilus* (Townsend *et al.* 2007) and *Phaenicophilus* (Sly *et al.* 2010), which include the additional intron loci rhodopsin intron 1 (Rho-1) and muscle-specific tyrosine kinase intron 4 (Musk-4). Haplotype networks are redrawn from and nucleotide variation statistics are reported from these previous sources. Divergence time estimates for *Phaenicophilus* are reported from

Table 2 Mitochondrial ND2 model-corrected divergence and time estimates. Time since divergence is calculated using 2.1% per million years and model-corrected divergences

Comparison	Model	Model values	Uncorrected divergence (%)	Model-corrected divergence (%)	Time (millions of years)	±0.1% (95% CI)
North paleo-island—South paleo-island						
*Calyptophilus**	K2 + G	Gamma = 0.25	11.8–12.9	21.7–25.9	10.3–12.3	9.9–13.0
Todus angustirostris	F81	n/a	2.9–3.8	3.0–4.0	1.4–1.9	1.4–2.0
Microligea	TN + G	Gamma = 0.769	0.9–1.6	0.9–1.6	0.4–0.8	0.4–0.8
Tiburon Peninsula—Mainland Hispaniola						
Phaenicophilus†	HKY + I + G	Gamma = 0.508 pINV = 0.197	5.3–5.9	6.6–7.7	3.1–3.7	3.0–3.9
Xenoligea	TN + G	Gamma = 0.769	0.6–0.8	0.6–0.8	0.3–0.4	0.3–0.4
Between endemic genera						
Microligea—Xenoligea	TN + G	Gamma = 0.769	16.4–17.0	21.7–22.8	10.3–10.9	9.9–11.4
P. palmarum—Microligea	TN + G	Gamma = 0.769	17.2–18.3	23.3–25.2	11.1–12.0	10.5–12.6
P. palmarum—Xenoligea	TN + G	Gamma = 0.769	17.9–18.5	25.2–26.4	12.0–12.6	11.5–13.2
P. poliocephalus—Microligea	TN + G	Gamma = 0.769	16.6–18.0	21.8–24.4	10.4–11.6	9.9–12.2
P. poliocephalus—Xenoligea	TN + G	Gamma = 0.769	17.6–18.1	24.4–25.6	11.6–12.2	11.1–12.8

*From Townsend *et al.* (2007).
†From Sly *et al.* (2010).

Sly *et al.* (2010). The mitochondrial clock divergence time estimate for *Calyptophilus* was not reported in Townsend *et al.* (2007) and is newly calculated here using the model-corrected divergence estimates reported in Townsend *et al.* (2007). The IMa divergence time estimates are reported from Townsend *et al.* (2007).

Results

Unique haplotypes and alleles have been archived in Genbank for each genus: *Calyptophilus* (accession numbers DQ152823, DQ166554–DQ166574, EF193693–EF193782; Townsend *et al.* 2007), *Phaenicophilus* (FJ159166–FJ159241; Sly *et al.* 2010), *Microligea* (HQ529945–HQ529967, HQ529982–HQ530005, HQ530076–HQ530105), *Xenoligea* (HQ529968–HQ529972, HQ530006–HQ530012, HQ530106–HQ530109, HQ530146–HQ530149), *Todus* (HQ529973–HQ529981, HQ530014–HQ530075, HQ530110–HQ530145), *Myadestes* (HQ529925–HQ529933), *Spindalis* (HQ529934–HQ529944) and *Elaenia* (HQ529917–HQ529924).

Haplotype patterns

Haplotype networks revealed one of three common patterns of historical divergence for each species comparison: divergence of haplotypes between the North and South paleo-islands (Fig. 2), divergence of haplotypes between the Tiburon Peninsula and the rest of Hispaniola (Fig. 3), or no divergence among populations across Hispaniola (Fig. 4). The divergence pattern in each species was strongest at the mitochondrial locus and shallower or not evident in the nuclear loci, a result consistent with the expectation from coalescent theory that the lower effective population size of mtDNA markers will cause them to coalesce more rapidly (Zink & Barrowclough 2008). The degree of divergence at the mitochondrial locus varied among the species exhibiting each pattern.

North and South paleo-island divergence. In *Todus angustirostris*, North and South paleo-island haplotypes of mitochondrial ND2 sequences (1032 bp, Fig. 2b) form reciprocally monophyletic clusters separated by 2.9–3.8% uncorrected divergence. Maximum uncorrected divergence within the North paleo-island cluster is 1.0% and within the South paleo-island cluster is 0.5%. No haplotypes are shared between South paleo-island populations, and two of four sampled North paleo-island populations share the most common haplotype, but sample sizes are too small for a robust evaluation of haplotype sharing among populations. Nuclear introns do not show monophyletic geographic segregation, but exhibit patterns of paraphyly. Only the most common alleles are shared between North and South paleo-island populations in Fib-5 (544 bp), but there is widespread allele sharing among populations within the North and South paleo-islands. There is no allele sharing between North and South paleo-island populations in Aco-9 (1051 bp) and extensive sharing of common alleles within North and South paleo-island populations, but the divergence is not monophyletic.

Microligea palustris lacks reciprocally monophyletic divergence of North and South paleo-island populations

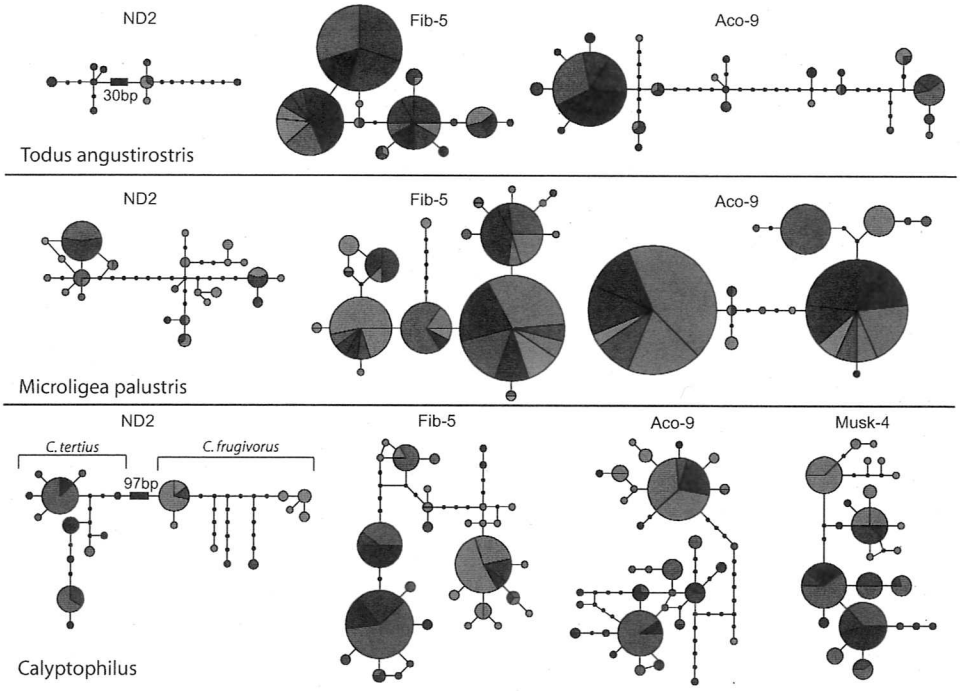

Fig. 2 Statistical parsimony haplotype networks for species with North/South phylogeographic structure—*Todus angustirostris*, *Microligea palustris* and *Calyptophilus*. Locality colours correspond to those in Fig. 1. South paleo-island haplotypes are coloured in reds and browns, and North paleo-island haplotypes are coloured in greens and blues. The black bars in *Calyptophilus* and *T. angustirostris* ND2 represent multiple nucleotide substitutions as indicated. *Calyptophilus* networks redrawn from Townsend *et al.* 2007.

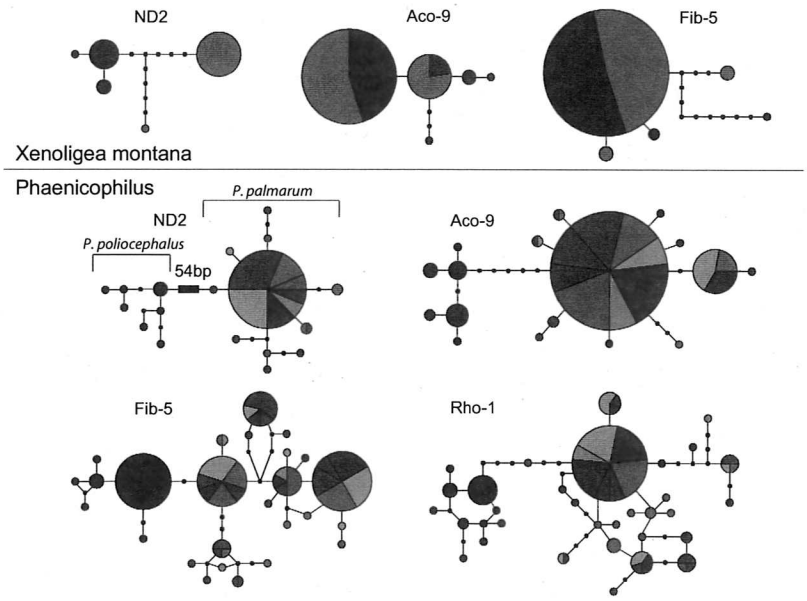

Fig. 3 Statistical parsimony haplotype networks for species with Tiburon Peninsula phylogeographic structure—*Xenoligea montana* and *Phaenicophilus*. The black bar in *Phaenicophilus* ND2 represents 54 nucleotide substitutions. Locality colours correspond to those in Fig. 1. Haplotypes from the Tiburon Peninsula (*P. poliocephalus*) are coloured dark red, South paleo-island localities are reds to browns, and North paleo-island localities are greens and blues. *Phaenicophilus* networks are redrawn from Sly *et al.* 2010.

in ND2 haplotypes (1053 bp), but distinct segregation occurs (maximum 1.5% uncorrected divergence, Fig. 2c) with haplotypes from individuals from Sierra de Neiba occurring in both the North and South paleo-island haplotype clusters. Common alleles are shared among most populations in both paleo-island groups. No phylogeographic divergence was present in Fib-5 (511 bp) or Aco-9 (1003 bp) for *Microligea*, and there is extensive allele sharing across all populations at most common alleles.

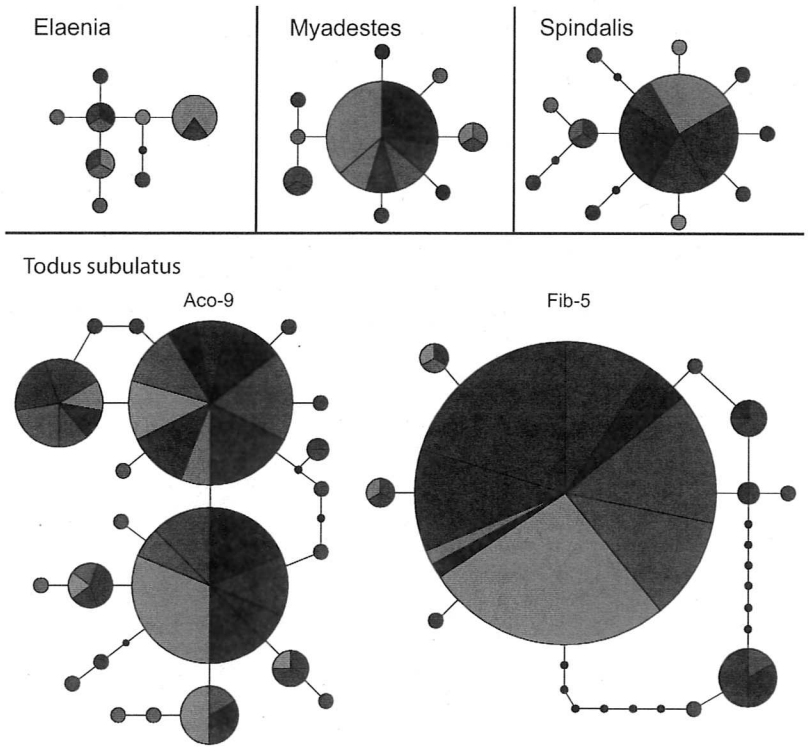

Fig. 4 Statistical parsimony haplotype networks for species with no phylogeographic structure—*Elaenia fallax, Myadestes genibarbis, Spindalis dominicensis* and *Todus subulatus*. Networks for *Elaenia, Myadestes* and *Spindalis* represent ND2. Networks for *Todus subulatus* represent the nuclear introns Aco-9 and Fib-5. Locality colours correspond to those in Fig. 1.

In comparison, Townsend *et al.* (2007) found that *Calyptophilus* shows strong evidence of historical divergence and speciation across the boundary between the North and South paleo-island, including substantial but not complete reciprocally monophyletic mitochondrial divergence (11.8–12.9% uncorrected) and geographic clustering in three nuclear intron loci. Haplotype networks are redrawn from Townsend *et al.* (2007) in Fig. 2a. Full details of these results are given in Townsend *et al.* (2007).

Tiburon Peninsula divergence. Haplotypes for *Xenoligea montana* show a reciprocally monophyletic split in ND2 between Tiburon Peninsula and Western Sierra de Bahoruco of 0.6–0.8% uncorrected divergence (1065 bp, Fig. 3a). No divergence between the two populations is evident at Aco-9 or Fib-5 (1003 and 510 bp, respectively, Fig. 3a), with sharing between the two populations at common alleles.

In comparison, Sly *et al.* (2010) found that *Phaenicophilus* ND2 haplotypes show strong reciprocally monophyletic divergence (5.3–5.9% uncorrected) between the Tiburon Peninsula population (*P. poliocephalus*) and the rest of the island (*P. palmarum*), and nuclear introns show congruent patterns. Haplotypes are redrawn from Sly *et al.* (2010) in Fig. 3b. Full details of these results are given in Sly *et al.* (2010).

No phylogeographic pattern. No phylogeographic structuring is apparent in ND2 in *Elaenia fallax* (Fig. 4a), *Myadestes genibarbis* (Fig. 4b) and *Spindalis domincensis* (Fig. 4c), or in nuclear intron loci for *Todus subulatus* (Fig. 4d), and within each of these taxa, there is extensive sharing of common haplotypes and alleles across populations.

Divergence time analyses

We used the mitochondrial clock and coalescent analyses to estimate divergence times between the North and South paleo-island groups within *Microligea palustris* and *Todus angustirostris* and between the Tiburon Peninsula and South paleo-island groups in *Xenoligea montana*. We also estimated the pairwise divergence times using the mitochondrial clock among the members of the Hispaniolan radiation of *Phaenicophilus, Microligea* and *Xenoligea*. The optimal models of sequence evolution in ND2 selected in TOPALi for each group are presented in Table 2 with the model-corrected divergences and divergence time estimates using the mitochondrial rate of 2.1% per million years.

The four-gamete test found evidence for recombination in Fib-5 and Aco-9 in both *Todus angustirostris* and *Microligea palustris*, but not in *Xenoligea montana*. Selecting the longest recombination-free segments reduced

the length of Fib-5 and Aco-9 in *Todus angustirostris* from 544 to 505 bp and 1051 to 409 bp, respectively, and in *Microligea palustris* from 511 to 324 bp and 1003 to 778 bp, respectively. The HKA tests were not significant at any locus in any species ($P > 0.05$), indicating that these segments are selectively neutral. Final IMa simulations with different random seeds produced convergence in parameter estimates. The results of the longest run for each comparison are presented as peak probabilities and 90% highest probability density (HPD) distributions of the six demographic parameters in Table 3 and as posterior probability density distributions for time and migration parameters in each comparison in Fig. 5. All probabilities are scaled to the neutral mutation rate (μ). Conversions of the peak probability and HPD of the time parameter to time since divergence measured in years are presented in Table 3. The geometric mean per-locus mutation rate used to convert the time estimates are 2.166×10^{-6} s/l/y for *Microligea palustris*, 2.752×10^{-6} s/l/y for *Xenoligea montana* and 2.008×10^{-6} s/l/y for *Todus angustirostris*.

The time parameter estimates did not produce a closed upper bound. They either reached a plateau at a probability lower than the unchanging peak across a range of upper bound priors (*Todus angustirostris*, Fig. 5c) or slowly declined in probability without reaching zero at high upper bound priors (Fig. 5a,b). These open probability distributions are not believed to bias the estimate of peak probability, but upper bound prior choice could affect the upper bound of the HPD intervals for the time parameters (Strasburg and Rieseburg 2009).

Discussion

Our examination of endemic bird taxa on Hispaniola reveals a consistent pattern: phylogeographic divergence within or between closely related species is correlated with the presence of ancient sea barriers. Adding seven species to two previously published studies of sister-species pairs (*Phaenicophilus*: Sly *et al.* 2010; *Calyptophilus*: Townsend *et al.* 2007), we find historical divergence correlates with either the divide between the North and South paleo-islands (*Calyptophilus, Microligea, Todus angustirostris*) or isolation on the Tiburon peninsula (*Phaenicophilus, Xenoligea*), whereas additional forms show no within-island phylogeographic divergence (*Todus subulatus, Spindalis, Elaenia, Myadestes*).

Timing of divergence

To correlate timing of divergence events with the presence of barriers to gene flow, we used two estimates of divergence time—the standard 2.1% mitochondrial

Table 3 Isolation with migration analysis parameter estimates—peak posterior probabilities with 90% highest probability densities in parentheses. Parameter estimates are scaled to the neutral mutation rate with the time parameter converted to units in years

Comparison	Q1	Q2	QA	M1	M2	T	T (millions of years)
North paleo-island—South paleo-island							
*Calyptophilus**	2.33 (1.35–3.39)	1.47 (0.80–2.2)	Not reported	0.065 (0.01–0.22)	0.445 (0.14–0.80)	Not reported	9.7 (6.6–27.1)
Todus angustirostris	5.0625 (2.7075–9.3375)	1.3960 (0.6200–2.9400)	6.0610 (0.0330–19.5910)	0.5625 (0.0175–1.4625)	0.4475 (0.0025–1.8225)	2.4600 (0.4200–39.9400)	1.2 (0.2–19.9)
Microligea	5.8575 (3.6075–9.8625)	1.2680 (0.5480–2.7960)	2.6325 (0.0075–11.9625)	0.1925 (0.0035–2.5585)	1.4460 (0.0060–5.7780)	0.4120 (0.1320–7.1320)	0.2 (0.1–3.3)
Tiburon Peninsula—Mainland Hispaniola							
Phaenicophilus†	2.1400 (1.3000–3.3720)	0.6457 (0.4760–1.8360)	0.9560 (0.0050–8.7650)	1.0113 (0.0005–0.5235)	0.2050 (0.0005–0.7105)	2.2700 (1.1300–19.0900)	2.2 (1.1–20.7)
Xenoligea	1.3845 (0.2405–4.5435)	0.3605 (0.06655–1.8095)	9.1125 (4.0875–64.9125)	0.0350 (0.0070–6.6990)	0.0070 (0.0070–10.6610)	0.9820 (0.0460–3.1100)	0.4 (0.02–1.1)

*From Townsend *et al.* (2007).
†From Sly *et al.* (2010).

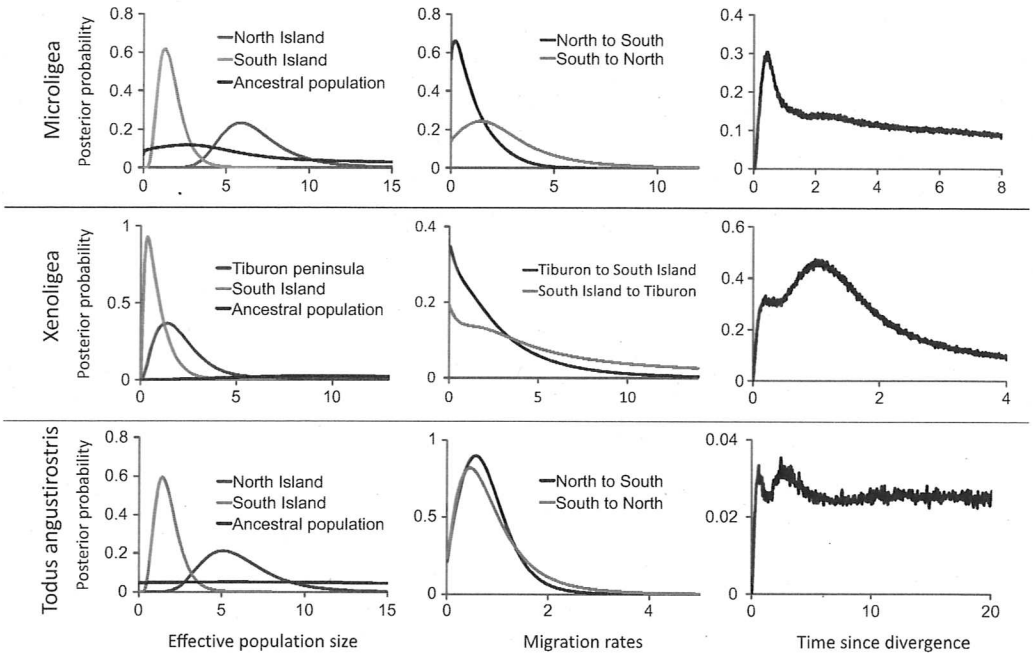

Fig. 5 Marginal posterior density distributions of demographic parameters from IMa analyses for *Microligea palustris*, *Xenoligea montana* and *Todus angustirostris*.

clock (Weir & Schluter 2008) and multilocus coalescent models in IMa utilizing general mutation rates for both mitochondrial and nuclear loci (the two estimates are not totally independent because the mitochondrial rate used in IMa is also 2.1%). Using mutation rates as molecular clocks to estimate divergence times is subject to large and difficult-to-calculate errors, including rate heterogeneity within and between lineages and loci and errors in the fossil and geographic calibrations necessary to 'set' the clock (Arbogast *et al.* 2002; Garcia-Moreno 2004; Lovette 2004). The 'standard' avian mitochondrial clock rate of 2.1% divergence per million years has been validated by a large number of calibrations, although rate variation among avian orders exists (Weir & Schluter 2008). The mutation rate used for nuclear loci is based on a large-scale comparison of turkey and chicken divergence (Ellegren 2007) and is dependent upon accurate dating of their divergence. These species are distantly related to those in this study and variation between lineages certainly exists; however, no other large-scale avian estimates are available. Given these caveats, our divergence time estimates should be taken only as a general approximation. In all cases, our two estimates were generally concordant, as the range of divergence times estimated by the 2.1% rule fell within the 90% HPD IMa time estimate (Tables 2 and 3).

Timing of divergence varied greatly among taxa across each historical barrier, arguing against a common event driving divergence in the Hispaniolan avifauna. The oldest divergence, in *Calyptophilus*, dates to *c.* 10 Ma, predating the merging of the North and South paleo-islands into present-day Hispaniola in the mid-Miocene (Graham 2003). This suggests allopatric divergence of *Calyptophilus* when Hispaniola existed as separate paleo-islands (Townsend *et al.* 2007). In contrast, North–South divergence in *T. angustirostris* dates to the middle Pleistocene (*c.* 1.5 Ma) and divergence in *Microligea palustris* dates to the late Pleistocene [*c.* 500 thousand years ago (Ka)], implicating a saltwater barrier to dispersal as the result of single or repeated flooding events in the present-day valley between the North and South islands (McLaughlin *et al.* 1991; Mann *et al.* 1991). Across the Tiburon Peninsula, timing of divergence in both *Phaenicophilus* and *Xenoligea* predates the final uplift of the sea channel that separated it from the mainland (100 Ka, Maurrasse *et al.* 1982), but these taxa did not diverge simultaneously: *Phaenicophilus* diverged *c.* 2 Ma, whereas *Xenoligea* diverged *c.* 500 Ka, suggesting species-specific patterns of colonization of the isolated Tiburon.

In contrast to these divergence events, the present-day distributions of three genera that arose from the oldest divergence events among avifauna on Hispaniola (*Phaenicophilus*, *Microligea*, and *Xenoligea*; ~10–13 Ma; Klein *et al.* 2004) do not correspond with any known geological barrier. All three genera are currently widespread across Hispaniola, with broad, continuous distributions

in multiple habitats (*Microligea* and *Phaenicophilus*) or with a montane distribution across all major ranges (*Xenoligea*) (Keith *et al.* 2003). The divergence of these three genera predates the merging of separate paleo-island blocks into present-day Hispaniola (>8 Ma, Graham 2003), suggesting that these taxa had considerable opportunity to diverge allopatrically on separate paleo-island blocks and that current distributions reflect species expansion after the blocks merged. Diversification within each of these genera, including speciation in *Phaenicophilus* and the shallow divergence seen in *Microligea* and *Xenoligea*, occurred much more recently and corresponds with more recent saltwater barriers.

Divergence and species ecology

Habitat diversity can drive speciation by providing unfilled niches, potentially creating a pattern of divergence independent of geologic barriers. In only one case did we find divergence between ecologically divergent taxa that did not correspond to geologic barriers: the sister species, *Microligea* (generalist) and *Xenoligea* (montane endemic). Divergence between these taxa (10–11 Ma, Table 2) occurred during the period of mountain formation on Hispaniola (from 20 to 8 Ma, Heubeck & Mann 1991). Although the age of the divergence suggests potential ecological divergence during mountain formation, several factors complicate this scenario. Both species' current distributions span both paleo-island blocks, with the highland *Xenoligea* occurring on isolated mountain ranges on each paleo-island block plus the isolated Tiburon Peninsula. Their divergence predates the merging of the paleo-islands (8 Ma, Graham 2003), indicating that divergence occurred when Hispaniola existed as at least three islands. Because parallel ecological divergence on three islands is unlikely, this implies that the current distributions of these taxa do not reflect those during their divergence. We suggest therefore that it is more likely that these species initially diverged in allopatry on separate island blocks. However, it is still likely that ecology played a role in speciation between *Microligea* and *Xenoligea*—ecological divergence achieved while isolated in allopatry can facilitate subsequent sympatric occurrence (Price 2008).

Montane specialist species, those restricted to high elevation areas that are separated by unsuitable habitat, may be more susceptible to vicariance and genetic divergence across their range than are habitat generalists (Wiens 2004). Generalist species might also mix populations and potentially erase genetic structure after the major barriers between paleo-islands were removed. However, we found highland and lowland species among taxa both with genetic structure (highland: *Calyptophilus, Todus angustirostris, Xenoligea*; lowland: *Phaenicophilus, Microligea*) and those without apparent structure (highland: *Spindalis, Myadestes, Elaenia*; lowland: *Todus subulatus*). Furthermore, we detected no evidence for population divergence between mountain ranges not formerly separated by a saltwater barrier. Widespread haplotype sharing among populations on each side of a saltwater barrier indicates insufficient historical isolation for divergence, and gene flow has probably recently homogenized these populations. The montane species we examined thus may be better dispersers or less limited by habitat than expected (Wiens 2004). Also, climatic shifts during glacial cycles probably lowered montane habitats, connecting habitats between currently isolated ranges and preventing the long-term isolation of mountain populations (Keith *et al.* 2003). The lowland populations with genetic structure do show signs of secondary contact after the removal of the saltwater barriers: *Phaenicophilus* species meet in a hybrid zone near the former sea channel that isolated *P. poliocephalus* on the Tiburon Peninsula (McDonald & Smith 1994), and *Microligea* shows evidence of gene flow with mitochondrial haplotypes from the South paleo-island cluster being present in the closest North paleo-island population, the Sierra de Neiba. Maintenance of genetic structure when the saltwater barriers are removed, as happened repeatedly during Pleistocene sea level changes and in the present day, is dependent upon isolating mechanisms evolved during periods of allopatry and dispersal rates across the reopened areas. The idiosyncratic nature of these processes is a likely cause of the different levels and timing of divergence in the species that diverged during flooding cycles.

Several of the montane species in this study that show no sign of genetic divergence, such as *Myadestes genibarbis* and *Elaenia fallax*, probably arrived on Hispaniola after it had merged into a single island, providing further evidence that the present-day topography of Hispaniola is not driving genetic divergence. Both species are part of recent Caribbean radiations: *Elaenia fallax* diverged *c.* 2.5 Ma (based on the 2.1% rule on uncorrected divergence in ND2 in Rheindt *et al.* 2008) from a clade of *Elaenia* that began diverging in the Caribbean *c.* 3.5 Ma (Rheindt *et al.* 2008), and *Myadestes genibarbis* diverged approximately 1.6 Ma from a clade that began diverging in the Caribbean approximately 6.5 Ma (Miller *et al.* 2007). In contrast to the endemic genera (*Calyptophilus, Microligea, Xenoligea, Phaenicophilus*), which represent lineages that have been present at least 10 million years, these species probably arrived well after the main island fusion and mountain formation on present-day Hispaniola, leaving only the most recent Pleistocene flooding events as potential sources of vicariance. Lineage age is thus a factor that has

limited divergence on Hispaniola by reducing exposure to historical vicariance events.

Taxonomic groups vary in their responses to the variety of factors influencing within-island speciation, depending on their life-history traits (Ricklefs & Lovette 1999; Losos & Parent 2010). In anoles, ecological diversity and specialization contribute to speciation within large islands in the Greater Antilles, but the predominant source of within-island diversity comes from geographic segmentation across different mountain ranges (Losos & Parent 2010). In contrast, snails in the Galapagos show speciation primarily because of habitat diversity, independent of area (Losos & Parent 2010; Parent & Crespi 2006). Similar to the pattern found in Greater Antillean anoles, our results indicate a strong role of island configuration and geologic history, rather than ecological diversity, in generating Hispaniola's endemic avifauna. Unlike anoles, avian diversification probably required marine barriers to segment populations. Experimental tests of avian dispersal suggest water can be a significant dispersal barrier to certain ecological guilds of birds, even over very short distances (Moore *et al.* 2008). Similarly, comparative analyses have suggested that water forms a greater barrier to dispersal in birds than some other taxonomic classes, leading to greater intra-archipelago speciation (Kisel & Barraclough 2010).

Conclusions

With its large size, complex topography and high number of avian endemics, present-day Hispaniola appeared to be a likely candidate for *in situ* speciation of avifauna. Indeed, broad comparative data (Kisel & Barraclough 2010) and a well-supported example of *in situ* speciation on Jamaica (Gill *et al.* 1973; Coyne & Price 2000), Hispaniola's smaller and less topographically complex neighbour argue for a minimum island size much smaller than Hispaniola's for *in situ* speciation to occur. Our evidence suggests, however, that divergence in Hispaniola's avifauna has probably occurred only when and where the island was segmented into multiple paleo-islands separated by sea barriers. We found no evidence that ecological or topographical complexity generated diversity, either by creating open niches or by restricting long-term gene flow. This suggests that Hispaniolan birds are capable of over-land dispersal sufficient to prevent divergence on the landmass of Hispaniola, but that sea incursions have presented substantial barriers to dispersal and gene flow. Conclusive examples of within-island speciation at this spatial scale are still rare, and our work underscores the need for further refinement of the speciation–area curve in birds. Our work also highlights the necessity of considering island geologic history while refining the speciation–area relationship in birds. The different geologic origins of Hispaniola's paleo-island blocks imply that divergence events that significantly predate the island block merging (i.e. divergence in *Calyptophilus*, and the radiation of genera in *Phaenicophilus*, *Microligea*, and *Xenoligea*) cannot be considered *in situ* divergence, but instead as interarchipelago speciation across smaller islands in the ancient Caribbean. Similarly, divergence in response to episodic island segmentation by marine flooding after island block merging could represent either *in situ* vicariance or interarchipelago speciation by dispersal among the three island blocks, but neither scenario represents true within-island avian speciation.

Acknowledgements

We thank the many people who assisted with field work on Hispaniola, particularly J Almonte, J Brocca, E Cuevas, E Fernandez, E Garrido, J Gerwin, J Goetz, J Klavins and R Ortiz. Authorization to conduct work in the Dominican Republic was provided by the Subsecretaria de Areas Protegidas and the Departamento de Vida Silvestre. Field studies in Haiti were authorized by the Ministry of Environment and Agriculture. We are especially grateful for logistical support in Haiti provided by Société Audubon Haiti, particularly P Bayard, J Vilmond and F Sergile. We thank CA Makarewich, LM Stenzler and AL Talaba for guidance and assistance with laboratory work and MD Carling for assistance with analysis. We thank J Weir and an anonymous reviewer for comments that improved this manuscript. This research was supported by the Hughes Scholar Program, the Dextra Undergraduate Research Fund, the College of Agriculture and Life Sciences of Cornell University, the Benning Fund, the Mario Einaudi Center for International Studies, the American Ornithologists' Union, the Tinker Foundation/Latin American Studies Program, the Ecology and Evolutionary Biology Department of Cornell University, NSF grants DEB-0515981 and DEB-0315218, the Blake Fund, the Carolyn Foundation, the Conservation and Research Foundation, the National Geographic Society, the Stewart Foundation, the Thomas Marshall Foundation and friends of the Vermont Center for Ecostudies. Statistical analyses were carried out, in part, using the resources of the Computational Biology Service Unit from Cornell University, which is partially funded by Microsoft Corporation.

References

Arbogast BS, Edwards SV, Wakely J, Beerli P, Slowinski JB (2002) Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics*, **33**, 707–740.

Barker FK, Vandergon AJ, Lanyon SM (2008) Assessment of species limits among yellow-breasted meadowlarks (*Sturnella* spp.) using mitochondrial and sex-linked markers. *Auk*, **125**, 869–879.

Brown RP, Hoskisson PA, Welton J-H, Baez M (2006) Geological history and within-island diversity: a debris

avalanche and the Tenerife lizard *Gallotia galloti*. *Molecular Ecology*, **15**, 3631–3640.

Clement M, Posada D, Crandall K (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, **9**, 1657–1660.

Coyne JA, Price TD (2000) Little evidence for sympatric speciation in birds. *Evolution*, **54**, 2166–2171.

Diamond JM (1977) Continental and insular speciation in Pacific island birds. *Systematic Zoology*, **26**, 263–268.

Eberhard JR, Bermingham E (2004) Phylogeny and biogeography of the Amazona ochrocephala complex. *Auk*, **121**, 318–332.

Ellegren H (2007) Molecular evolutionary genomics of birds. *Cytogenetic and Genome Research*, **117**, 120–130.

Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**, 116–121.

Garcia-Moreno J (2004) Is there a universal mtDNA clock for birds? *Journal of Avian Biology*, **35**, 465–468.

Gifford ME, Larson A (2008) In situ genetic differentiation in a Hispaniolan lizard (*Ameiva chrysolaema*): a multilocus perspective. *Molecular Phylogenetics and Evolution*, **49**, 277–291.

Gifford ME, Powell R, Larson A, Gutberlet RL (2004) Population structure and history of a phenotypically variable teiid lizard (*Ameiva chrysolaema*) from Hispaniola: the influence of a geologically complex island. *Molecular Phylogenetics and Evolution*, **32**, 735–748.

Gill FB, Stokes FJ, Stokes C (1973) Contact zones and hybridization in the Jamaican Hummingbird, *Trochilus polytmus* (L.). *Condor*, **75**, 170–176.

Gillespie RG, Baldwin BG (2010) Island biogeography of remote archipelagoes. In: *The Theory of Island Biogeography Revisited* (eds Losos JB, Ricklefs RE), pp. 358–387. Princeton University Press, Princeton, NJ.

Glor RE, Kolbe JJ, Powell R, Larson A, Losos JB (2003) Phylogenetic analysis of ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). *Evolution*, **57**, 2383–2397.

Glor RE, Gifford ME, Larson A *et al.* (2004) Partial island submergence and speciation in an adaptive radiation: a multilocus analysis of the Cuban green anoles. *Proceedings of the Royal Society of London B*, **271**, 2257–2265.

Graham A (2003) Geohistory models and Cenozoic paleoenvironments of the Caribbean region. *Systematic Botany*, **28**, 378–386.

Heubeck C, Mann P (1991) Structural geology and Cenozoic tectonic history of the southeastern termination of the Cordillera Central, Dominican Republic. In: *Geological Society of America Special Papers, Vol. 262. Geologic and Tectonic Development of the North American–Caribbean Plate Boundary in Hispaniola* (eds Mann P, Draper G, Lewis JF), pp. 315–336. Boulder, CO.

Hey J, Nielsen R (2004) Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics*, **167**, 747–760.

Hey J, Nielsen R (2007) Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 2785–2790.

Hudson RR, Kaplan NL (1985) Statistical properties of the number of recombination events in the history of a sample of DNA sequences. *Genetics*, **111**, 147–164.

Hudson RR, Kreitman M, Aguade M (1987) A test of neutral molecular evolution based on nucleotide data. *Genetics*, **116**, 153–159.

Keith AR, Wiley JW, Latta SC, Ottenwalder JA (2003) *The Birds of Hispaniola*. British Ornithologists' Union, Tring, UK.

Kisel Y, Barraclough TG (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **175**, 316–334.

Klein NK, Burns KJ, Hackett SJ, Griffiths CS (2004) Molecular phylogenetic relationships among the wood warblers (Parulidae) and historical biogeography in the Caribbean basin. *Journal of Caribbean Ornithology*, **17**, 3–17.

Latta SC, Rimmer CC, McFarland KP (2003) Winter bird communities in four habitats along an elevational gradient on Hispaniola. *Condor*, **105**, 179–197.

Lomolino MV (2000) Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography*, **27**, 17–26.

Losos JB, Parent CE (2010) The speciation–area relationship. In: *The Theory of Island Biogeography Revisited* (eds Losos JB, Ricklefs RE), pp. 415–438. Princeton University Press, Princeton, NJ.

Losos JB, Schluter D (2000) Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847–850.

Lovette IJ (2004) Mitochondrial dating and mixed support for the "2% rule" in birds. *Auk*, **121**, 1–6.

Lovette IJ, Rubenstein DR (2007) A comprehensive molecular phylogeny of the starlings (Aves: Sturnidae) and mockingbirds (Aves: Mimidae): congruent mtDNA and nuclear trees for a cosmopolitan avian radiation. *Molecular Phylogenetics and Evolution*, **44**, 1031–1056.

Mann P, Draper G, Lewis JF (1991) An overview of the geologic and tectonic development of Hispaniola. In: *Geological Society of America Special Papers, Vol. 262. Geologic and Tectonic Development of the North American–Caribbean Plate Boundary in Hispaniola* (eds Mann P, Draper G, Lewis JF), pp. 1–28. Boulder, CO.

Maurrasse F, Pierre-Louis F, Rigaud J-G (1982) Cenozoic facies distribution in the Southern Peninsula of Haiti and the Barahona Peninsula, Dominican Republic. *Carib Geol Coll Contr*, **9**, 161–174.

McDonald MA, Smith MH (1994) Behavioral and morphological correlates of heterochrony in Hispaniolan Palm-Tanagers. *Condor*, **96**, 433–446.

McLaughlin PP, van den Bold WA, Mann P (1991) Geology of the Azua and Enriquillo basins, Dominican Republic; 1, Neogene lithofacies, biostratigraphy, biofacies, and paleogeography. In: *Geological Society of America Special Papers, Vol. 262. Geologic and Tectonic Development of the North American–Caribbean Plate Boundary in Hispaniola* (eds Mann P, Draper G, Lewis JF), pp. 337–366. Boulder, CO.

Mila B, Warren BH, Heeb P, Thebaud C (2010) The geographic scale of diversification on islands: genetic and morphological divergence at a very small spatial scale in the Mascarene grey white-eye (Aves: *Zosterops borbonicus*). *BMC Evolutionary Biology*, **10**, 158.

Miller MJ, Bermingham E, Ricklefs RE (2007) Historical biogeography of the New World solitaires (*Myadestes* spp.). *Auk*, **124**, 868–885.

Milne I, Lindner D, Bayer M *et al.* (2009) TOPALi v2: a rich graphical interface for evolutionary analyses of multiple alignments on HPC clusters and multi-core desktops. *Bioinformatics*, **25**, 126–127.

Moore RP, Robinson WD, Lovette IJ, Robinson TR (2008) Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, **11**, 960–968.

Nielsen R, Wakely J (2001) Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics*, **158**, 885–896.

Overton LC, Rhoads DD (2004) Molecular phylogenetic relationships based on mitochondrial and nuclear gene sequences for the Todies (Todus, Todidae) of the Caribbean. *Molecular Phylogenetics and Evolution*, **32**, 524–538.

Parent CE, Crespi BJ (2006) Sequential colonization and diversification of Galapagos endemic land snail genus Bulimulus (Gastropoda, Stylommatophora). *Evolution*, **60**, 2311–2328.

Price T (2008) *Speciation in Birds*. Roberts and Company, CO.

Rheindt FE, Christidis L, Norman JA (2008) Habitat shifts in the evolutionary history of a Neotropical flycatcher lineage from forest and open landscapes. *BMC Evolutionary Biology*, **8**, 193.

Ricklefs RL, Bermingham E (1997) Molecular phylogenetics and conservation of Caribbean birds. *El Pitirre*, **10**, 85–92.

Ricklefs RE, Lovette IJ (1999) The roles of island area per se and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology*, **68**, 1142–1160.

Rimmer CC, Almonte JM, Garrido EG, Mejia DA, Milagros MP, Wieczoreck PR (2003) Bird records in a montane forest fragment of western Sierra de Neiba, Dominican Republic. *Journal of Caribbean Ornithology*, **16**, 55–60.

Rimmer CC, Townsend JM, Townsend AK, Fernandez EM, Almonte J (2005) Avian diversity, abundance, and conservation status in the Macaya Biosphere Reserve of Haiti. *Ornitologia Neotropical*, **16**, 219–230.

Rozas J, Sanchez-DelBarrio JC, Messeguer X, Rozas R (2003) DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics*, **19**, 2496–2497.

Ryan PG, Bloomer P, Moloney CL, Grant TJ, Delport W (2007) Ecological speciation in south Atlantic island finches. *Science*, **315**, 1420–1423.

Sly ND, Townsend AK, Rimmer CC, Townsend JM, Latta SC, Lovette IJ (2010) Phylogeography and conservation of the endemic Hispaniolan Palm-Tanagers (Aves: *Phaenicophilus*). *Conservation Genetics*, **11**, 2121–2129.

Sorenson MD, Quinn TW (1998) Numts: a challenge for avian systematics and population biology. *Auk*, **115**, 214–221.

Stephens M, Scheet P (2005) Accounting for decay of linkage disequilibrium in haplotype inference and missing data imputation. *American Journal of Human Genetics*, **76**, 449–462.

Stephens M, Smith NJ, Donnelly P (2001) A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, **68**, 978–989.

Strasburg JL, Rieseburg LH (2009) How robust are "Isolation with Migration" analyses to violations of the IM model? A simulation study. *Mol Biol Evol*, **27**, 297–310.

Swofford DL (2000) *PAUP*: Phylogenetic Analysis Using Parsimony and Other Methods*. Sinauer Associates, Sunderland, MA.

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, **24**, 1596–1599.

Townsend JM, Rimmer CC (2006) Known natal and wintering sites of a Bicknell's Thrush. *Journal of Field Ornithology*, **77**, 452–454.

Townsend AK, Rimmer CC, Latta SC, Lovette IJ (2007) Ancient differentiation in the single-island avian radiation of endemic Hispaniolan chat-tanagers (Aves: Calyptophilus). *Molecular Ecology*, **16**, 3634–3642.

Weir JT, Schluter D (2008) Calibrating the avian molecular clock. *Molecular Ecology*, **17**, 2321–2328.

White PS, Densmore LD (1992) Mitochondrial DNA isolation. In: *Molecular Genetic Analysis of Populations* (ed. Hoelzel AR), pp. 29–58. Oxford University Press, New York.

Wiens JJ (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, **58**, 193–197.

Zink RM, Barrowclough GF (2008) Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology*, **17**, 2107–2121.

Supporting information

Additional supporting information may be found in the online version of this article.

Data S1 Individual sample locations, blood numbers, and Genbank accession numbers for each locus.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.