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Origin, paleoecology, and extirpation of bluebirds and crossbills in the Bahamas across the last glacial–interglacial transition

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On low islands or island groups such as the Bahamas, surrounded by shallow oceans, Quaternary glacial–interglacial changes in climate and sea level had major effects on terrestrial plant and animal communities. We examine the paleoecology of two species of songbirds (Passeriformes) recorded as Late Pleistocene fossils on the Bahamian island of Abaco—the Eastern bluebird (*Sialia sialis*) and Hispaniolan crossbill (*Loxia megaplaga*). Each species lives today only outside of the Bahamian Archipelago, with *S. sialis* occurring in North and Central America and *L. megaplaga* endemic to Hispaniola. Unrecorded in the Holocene fossil record of Abaco, both of these species probably colonized Abaco during the last glacial interval but were eliminated when the island became much smaller, warmer, wetter, and more isolated during the last glacial–interglacial transition from ~15 to 9 ka. Today’s warming temperatures and rising sea levels, although not as great in magnitude as those that took place from ~15 to 9 ka, are occurring rapidly and may contribute to considerable biotic change on islands by acting in synergy with direct human impacts.

Bahamas | bluebird | crossbill | extirpation | island biogeography

Most of the documented late Quaternary extirpation of insular birds and other vertebrates took place during the Holocene after the arrival of humans (1). While this statement holds true on West Indian islands as much as on any other set of islands (2–4), an ice age (Pleistocene glacial interval; >9 ka, but not precisely dated) vertebrate fauna from Sawmill Sink, a blue hole on Abaco Island in the northern Bahamas, featured 17 resident species of birds known from Abaco only as Pleistocene fossils (5). None of these 17 species have been recorded in Abaco’s record of Holocene bird fossils, dated to ≤5 ka (3, 6). This paper will focus on two of the Pleistocene bird populations that likely were lost to changes in climate and sea level that took place during the Pleistocene–Holocene transition (PHT) from ~15 to 9 ka, well before any human presence in the Bahamas.

Some longer-term perspective is warranted. Estimates of sea-level highstands during marine isotope stage (MIS) 11 (~410–400 ka) vary from +5 to +20 m above modern sea level with most studies yielding estimates from +6 to +13 m (7–10). These high sea levels would have eliminated most land and most if not all resident nonmarine bird populations that had existed in the Bahamas during the previous glacial interval. Since MIS 11, the bird community during each ice age (glacial interval) and subsequent interglacial interval in the Bahamas was undoubtedly different because of species-level variation in colonization and extinction during each of the major changes in sea level, land area (Fig. 1), climate, and habitat. The only time subsequent to MIS 11 when sea levels were clearly higher than today (+3 to +6 m) was during MIS 5e (~131–119 ka or 124–115 ka) (11, 12); MIS 5e would have been the last time that the land area of the Bahamas was smaller than it is now (13).

We will examine the origin, paleoecology, and extirpation of the Eastern bluebird (*Sialia sialis*; Turdidae) and Hispaniolan crossbill (*Loxia megaplaga*; Fringillidae). Fossils from Sawmill

Sink are the only evidence that either of these species ever resided in the Bahamas. We chose these species to compare the paleobiology of two extirpated passerines, one restricted today to continents and the other to an island. Breeding populations of *S. sialis* are confined today to continental North and Central America (Fig. 2). (The population on Bermuda arrived there within the past 400 y, with human assistance) (14). Vagrant (nonbreeding) records of *S. sialis* exist from the Bahamas (Harbour Island off Eleuthera) (15), Cuba, and St. John in the Virgin Islands (16). *Loxia megaplaga* is endemic to the island of Hispaniola (Haiti + Dominican Republic) with a possible vagrant record from Jamaica (16, 17). The two other New World species of *Loxia* are continental (Fig. 3 and *SI Appendix*, Fig. S1).

Modern populations of any species of *Sialia* or *Loxia* are either residents or short-distance diurnal migrants–wanderers. Our two focal species differ substantially in their feeding and nesting ecology. The Eastern bluebird occupies open-canopy woodlands with grassy understories, where they are sit-and-wait foragers pursuing insects and fruits, primarily on the ground (18–20). Eastern bluebirds are obligate cavity nesters. The Hispaniolan crossbill, which builds cup nests, requires pine trees (*Pinus occidentalis*) for both foraging and nesting (21, 22). This crossbill subsists on seeds of the pine tree *P. occidentalis* (also endemic to Hispaniola), extracting the seeds from cones with its crossed rostrum and mandible (23). The density of pine trees in the Hispaniolan crossbill’s montane habitat can vary from a nearly closed-canopy forest to an open woodland (21).

Significance

On tropical islands, extensive extirpation of birds and other vertebrates occurred during the Holocene, following human arrival. Much less is known about pre-Holocene extirpation on islands. We focus on two species (Eastern bluebird *Sialia sialis* and Hispaniolan crossbill *Loxia megaplaga*) that were lost in the Bahamas to changes in sea level (becoming higher), land area (getting smaller), climate (becoming warmer and wetter), and habitat (loss of pine grassland) that took place during the last glacial–interglacial transition, many millennia before peopling of the islands. While volant, the bluebird evolved a short wing in the Bahamas, whereas the crossbill retained a similar morphology to the surviving population on Hispaniola. Each major glacial–interglacial shift reconfigured the resident Bahamian flora and fauna.

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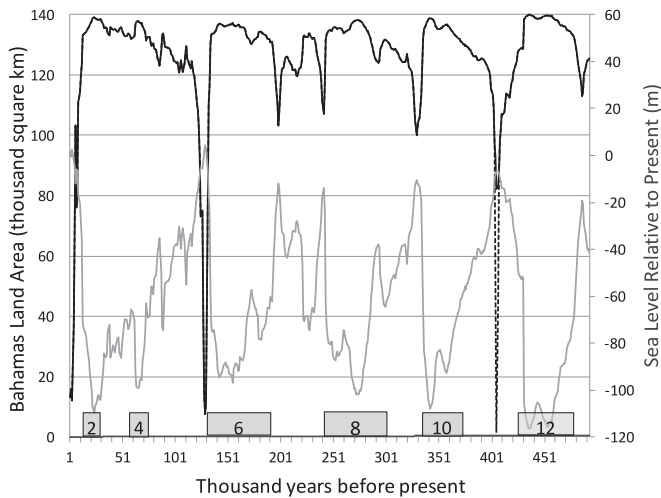


Fig. 1. Changing sea level (from ref. 51) and estimated land area (estimated from ref. 52) of the Bahamian Islands. Dashed line shows estimated land area (54 km^2) +20 m at 404 ka BP (MIS11). Approximate dates of even-numbered (glacial) marine isotope stages (MISs) are shown for reference.

Since its description a century ago (24), many authors (e.g., ref. 25) have followed Bond (26) in considering *L. megaplaga* to be a subspecies of the white-winged crossbill (*Loxia leucoptera*), which otherwise inhabits boreal or cool temperate parts of North America (*L. l. leucoptera*) and Eurasia (the larger *L. l. bifasciata*). We follow Wetmore and Swales (27) in regarding *L. megaplaga* as endemic to Hispaniola, a judgment supported by molecular data (28, 29) and osteological data presented in this paper.

Through comparative osteology, we document morphological differences between the ice age populations of bluebirds and crossbills in the Bahamas and extant conspecific (bluebirds) or congeneric (crossbills) populations on the mainland. We then will evaluate why bluebirds and crossbills did not survive in the Bahamas during the last glacial–interglacial shift, which was the PHT from ~ 15 –9 ka. We will consider changes in sea level and land area associated with glacial–interglacial cycles over the last $\sim 500,000$ y. We also will use species distribution and paleodistribution modeling (30, 31) to compare the climatic conditions occupied by extant conspecific and congeneric populations (evaluated at the subspecies level) with the current climatic and paleoclimatic conditions of the Bahamas during glacial intervals, represented by the Last Glacial Maximum (LGM; ~ 25 –18 ka).

Results

Bluebirds. We assign 35 Bahamian fossils (eight different skeletal elements) to the Eastern bluebird (*S. sialis*) based on a combination of 13 osteological characters from six skeletal elements that distinguish them from other turdine genera (Table 1). Among the three species of *Sialia*, the fossils agree with *S. sialis* in the proportions of the humerus, ulna, and carpometacarpus (stouter in *Sialia mexicanus*, more slender in *Sialia curricoides*). We found no intraspecific features in any single skeletal element to distinguish the Bahamian fossils from any living form of *S. sialis*. The bluebird fossils from Abaco also are similar in overall size to the modern bones of *S. sialis* from the North and Central American mainland (Fig. 4), except that females of *S. s. fulva* average smaller than all others (*SI Appendix, Table S1*). Nevertheless, the Bahamian bluebird fossils do differ from all other forms of *S. sialis* in having a relatively short distal wing (low ratio of carpometacarpus length to humerus length; an exception being the single specimen of *S. s. guatemalae* from Chiapas) and a relatively large body for its wing size (high ratio of femur length to humerus length (32), although these ratios are not necessarily

based on bones from the same individuals. These trends in the limb proportions of Bahamian Eastern bluebirds, which are to be expected in resident insular versus continental populations of conspecific volant songbirds (32, 33), were not evident in the two bluebird skeletons from Bermuda (*SI Appendix, Table S1*).

The subspecies *S. s. fulva* (southwestern United States and northwestern Mexico) and *S. s. guatemalae* + *S. s. meridionalis* are predicted to have very low average per-area climate suitability in modern Bahamas (0.003 and 0.007, respectively, relative likelihood of occurrence, scale 0–1; *SI Appendix, Table S2*) and higher in the ice age Bahamas based on species distribution models (SDMs) projected to LGM climates for at least one climate model, but still with low suitability (0.006–0.024). The area-summed suitability of the ice age Bahamas is predicted to be ~ 5 –80 times greater than at present, primarily because of the greater land area (*SI Appendix, Table S3*). The subspecies combination *S. s. episcopus* + *S. s. sialis* shows a similar pattern (0.048 for the current climate vs. 0.026–0.114 for LGM climate). Thus, the paleodistribution models provide no strong evidence for which subspecies of *S. sialis* might have colonized Abaco. *Sialia s. grata* (confined to Florida, questionably distinct from *S. s. sialis*) (19) is the subspecies of Eastern bluebird whose modern distribution shares the most similar climate to the modern in Bahamas (0.231), but the SDMs predict it to have lower climatic suitability in Bahamas at the LGM than at present (0.020–0.058; *SI Appendix, Table S2*). Even *S. s. grata* is predicted to have a greater area-summed climatic suitability at the LGM (*SI Appendix, Table S3*) because of the much greater land area in the Bahamas at that time (Fig. 1).

Crossbills. The crossbill fossils from Abaco (eight specimens, four skeletal elements) include a complete mandible (Fig. 5) that shares two of three characters with modern specimens of the Hispaniolan crossbill *L. megaplaga* (Table 2). In size, the Bahamian crossbill fossils also resemble both modern and fossil *L. megaplaga* specimens from Hispaniola (*SI Appendix, Table S4*). This species is much larger than in any modern specimens of *L. leucoptera*, its continental sister species based on molecular data (28, 29) and plumage (white wing bars). James (34) distinguished *L. leucoptera* from *Loxia curvirostra* by the number of fused thoracic vertebrae in the notarium (three in the former, two in the latter). We find that the number is three in *L. megaplaga*, further supporting its close relationship with *L. leucoptera*.

Modern specimens of *L. curvirostra*, especially the relatively large *L. c. stricklandi*, resemble in size the modern and fossil

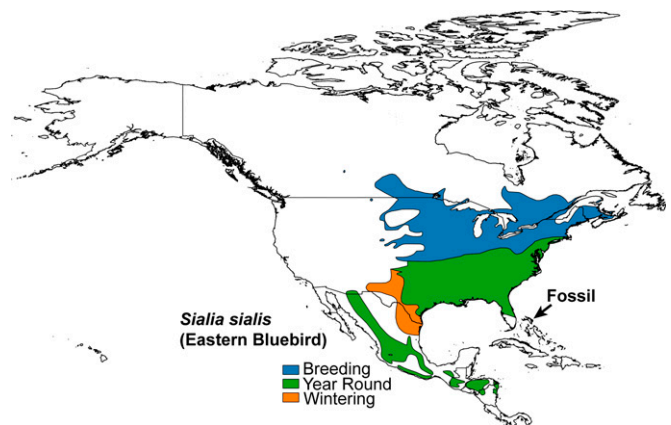


Fig. 2. Modern distribution of the Eastern bluebird (*S. sialis*), noting its fossil occurrence on Abaco. Modified from the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, version 2016–3. <www.iucnredlist.org>, downloaded on April 5, 2017.

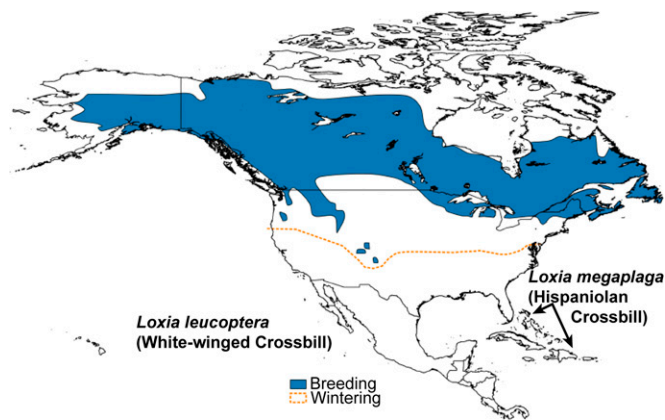


Fig. 3. Modern distribution of the white-winged crossbill (*L. leucoptera*; continental) and the Hispaniolan crossbill (*L. megaplaga*; insular, with both modern and fossil records from Hispaniola, and fossil records only from the Bahamas). “Wintering” (nonbreeding) range is highly variable from year to year. Modified from the IUCN Red List of Threatened Species, version 2016–3. <www.iucnredlist.org>, downloaded on April 5, 2017.

specimens of *L. megaplaga* more than *L. leucoptera* (*SI Appendix, Figs. S2–S4 and Table S4*). The crossbill fossils from the Bahamas and Haiti have a slightly larger body for its wing size compared with others (high ratio of tibiotarsus length to humerus length; *SI Appendix, Figs. S3 and S4 and Table S4*; femur not available in fossils). As with Eastern bluebirds, resident populations of *L. curvirostra* exist today in southern Mexico and northern Central America (35), including in lowland savannas and woodlands featuring Caribbean pine (*Pinus caribaea*), the same species as occurs in the Bahamas (36). Thus, we evaluated the SDM for *L. curvirostra* as well as that of *L. l. leucoptera*. Among the subspecies of *L. curvirostra*, the model based on modern distribution of *L. c. mesoamericana* + *L. c. stricklandi* shows the highest climatic suitability in the Bahamas based on modern climate, but

still is low (median 0.055). Under three LGM climate models, the Bahamas are climatically much more suitable for these combined subspecies (median 0.093–0.133) because of higher per-area suitability (*SI Appendix, Table S2*) and greater insular land area (Fig. 1 and *SI Appendix, Table S3*).

L. l. leucoptera, with a high latitude distribution in North America (Fig. 3), shows no similarity in climatic conditions to the modern Bahamas, and average climatic suitability for the LGM also was very low (0.002–0.009), which is lower than for all but three of the *L. curvirostra* subspecies (*SI Appendix, Table S2*). The low SDM climatic suitability of *L. l. leucoptera* shows that these values may not be evidence of source area of the extirpated Bahamian population.

Compared with *Pinus occidentalis* measured on Hispaniola (ref. 29, table 2 therein), *P. caribaea* var. *bahamensis*, the only pine in the Bahamas, has cones that average longer but not wider or heavier, cone scales that are thinner, and seeds that are much lighter (*SI Appendix, Table S5*). Scale thickness of the Bahamian pine falls between the values for *Pinus cubensis* and *P. occidentalis* measured by Parchman et al. (29), who argued that the thick scales of *P. occidentalis* (thicker than in *P. cubensis*) had evolved as a defense to seed predation by *L. megaplaga*.

Discussion

Origin of Bluebird and Crossbill Populations in the Bahamas. The tectonically stable (37) Bahamian islands never have been connected directly to North America, Cuba, or Hispaniola, even during the LGM (26.5–19.0 ka) (38), when sea level was as much as 120 m lower than today (39) (Fig. 6). Dispersal among these geologically distinctive places, as well as among the low, geologically uniform islands sitting atop the carbonate banks of the Bahamas, involved shorter distances during glacial than interglacial times but still required the birds to fly over the ocean (ref. 6, tables S2 and S3 therein).

For Eastern bluebirds (*S. sialis*), the extirpated Bahamian population is not clearly attributable to any particular mainland form based on morphology or climatic similarity. Colonization of

Table 1. Generic-level comparative osteology of New World thrushes

Character	Bahamian fossils + <i>Sialis</i>	<i>Catharus</i> + <i>Hylocichla</i>	<i>Myadestes</i>	<i>Turdus</i>
CORACOID				
Facies articularis clavicularis in ventral aspect	Straight; perpendicular to corpus coracoidei	Curved; pointed	Curved; pointed	Curved; pointed
Medial surface of clavicular end of corpus coracoidei	Sharp	Rounded	Rounded	Rounded
HUMERUS				
Junction of crista bicipitalis and corpus humeri in caudal aspect	Gradual	Less obtuse angle	Gradual	Gradual
Medial fossa pneumotricipitalis	Shallower	Deeper	Deeper	Deeper
ULNA				
Junction of cotyla dorsalis and corpus ulnae in medial or cranial aspect	Gradual	Abrupt	Abrupt	Abrupt
Sulcus radialis	Deep	Shallow	Deep	Shallow
CARPOMETACARPUS				
Orientation of processus extensorius	Nearly perpendicular	More medially directed	More medially directed	More medially directed
Facies articularis digitalis minoris	Short, stout	Long, slender	Long, slender	Intermediate
FEMUR				
In lateral aspect, protrusion of crista tibiofibularis beyond trochlea fibularis	Slight	Much	Much	Much
In lateral aspect, pointedness of trochlea fibularis	More rounded	More pointed	More pointed	More rounded
TIBIOTARSUS				
Overall stoutness of corpus tibiotarsi	Stout	Slender	Slender	Stout
Lateral protrusion of crista fibularis	Much	Slight	Much	Much
In distal aspect, depth of sulcus cartilaginis	Shallow	Deep	Deep	Deep



Fig. 4. Fossil (Abaco, Bahamas; Left; UF 312822–312824) and modern (Florida; Right; UF 46724) bones of the Eastern bluebird (*S. sialis*). (A) Humerus in anconal aspect. (B) Carpometacarpus in ventral aspect. (C) Femur in posterior aspect.

Abaco was more likely during glacial times because of closer proximity to North America, especially Florida (~75 km; ref. 6, tables S2 and S3 therein), the much larger land area of the Little Bahama Bank (Fig. 6), and Abaco's widespread pine grasslands. The LGM habitat of Florida has been interpreted as an open conifer woodland dominated by pine (40), just as in the Bahamas. Which other islands in the Bahamas may have been colonized by bluebirds awaits further fossil studies. The Hispaniolan crossbill (*L. megaplaga*) probably colonized the Little Bahama Bank from Hispaniola by island-hopping across the Great Bahama Bank where it likely also resided, although this has yet to be confirmed by fossils. Both colonization events must have taken place after the sea-level highstand of MIS 5e (~120 ka) but well before that of MIS 1 (~15–0 ka; ref. 41) (Fig. 1).

Extirpation of Bluebirds and Crossbills in the Bahamas. In the few places where they have been documented by fossils, the composition of late Pleistocene passerine bird communities on the neotropical mainland was very different from those existing in the same places today (42–44). Thus, it should be little surprise that the same holds true on neotropical islands. Neither *S. sialis* nor *L. megaplaga* are likely to have survived on Abaco after the Pleistocene–Holocene Transition (PHT) in climate, habitat, and island area that took place from ~15–9 ka. The PHT on Bahamian islands such as Abaco was characterized by major changes in climate (becoming more warm and moist), habitat (expanded coverage by broadleaf forest at the expense of pine woodland), sea level (rising from –80 m to nearly modern levels), and island area (being reduced from ~17,000 km² to 1,214 km²) (6). These land area values are just for Abaco–Little Bahama Bank; for the entire Bahamian Archipelago, the land area was reduced from ~130,000 km² to ~13,000 km²; Fig. 1).

On the much smaller, more isolated island of Bermuda, fossil deposits from dated Quaternary contexts provide ample evidence of glacial–interglacial changes in the vertebrate community, especially birds. For example, a breeding population of short-tailed albatross (*Phoebastria albatrus*), represented by fossils of embryos, juveniles, and adults, was eliminated on Bermuda by a sea-level highstand during MIS 11 at ~405 ka (45). Other species of reptiles and birds (mostly endemic) were lost from Bermuda during this and subsequent sea-level highstands, such as a tortoise (*Hesperotestudo*), a skink (*Eumeces*), and numerous birds, including rails (*Rallus*, *Porzana*, and *Gallinula*), a crane (*Grus*), a night heron (*Nyctanassa*), great auk (*Pinguinus impennis*), a duck (*Anas*), a crow (*Corvus*), and a towhee (*Pipilo*) (46, 47). Because Bermuda does not lie nearly as close to other,

higher islands (Cuba and Hispaniola) or to the North American continent as the Bahamian islands, the glacial–interglacial turnover in its bird communities probably was more drastic, lacking nearby landmasses where volant species perhaps could survive when land areas were reduced.

By inference with the habitat preferences of living populations, the relative abundance of fossils from Sawmill Sink of Eastern bluebirds ($n = 35$) and Hispaniolan crossbills ($n = 8$) suggests that the dominant late Pleistocene terrestrial habitat on Abaco was pine woodland with a grassy understory or a mosaic of pine woodland and grassland. This idea is reinforced by co-occurring late Pleistocene fossils at Sawmill Sink of nine other species of songbirds with similar habitat affinities (5), namely, Eastern meadowlark (*Sturnella magna*; $n = 1,075$), brown-headed nuthatch (*Sitta pusilla*; $n = 20$), chipping sparrow (*Spizella passerina*; $n = 12$), pine warbler (*Dendroica/Setophaga pinus*; $n = 10$), loggerhead kingbird (*Tyrannus caudifasciatus*; $n = 6$), “greater Antillean” oriole (*Icterus* cf. *dominicensis* species group; $n = 4$), yellow-throated/Bahama warbler (*D./S. dominica/flavescens*; $n = 3$), Savannah sparrow (*Passerculus sandwichensis*; $n = 2$), and grasshopper sparrow (*Ammodramus savannarum*; $n = 1$). Six of these 10 species no longer occur on Abaco (6). Along with the abundant fossils of burrowing owl (*Athene cunicularia*; $n = 1,914$), the passerine species strongly support the idea that the dominant late Pleistocene habitat on Abaco (and probably most other Bahamian islands) was a grassy pine woodland.

In North America, *Loxia l. leucoptera* feeds mostly on seeds of spruce (*Picea* spp.) and larch (*Larix laricina*) (25). Neither spruce nor larch occurs on Hispaniola or the Bahamas, where the only common conifers are pines (*P. occidentalis* on Hispaniola, *P. caribaea* in the Bahamas). (The Eastern red cedar (*Juniperus virginiana*) is listed as an occasional food for *L. l. leucoptera* in North America (25). The closely related *J. barbadensis* var. *lucayana* occurs in the Bahamas, where it may have supplemented the diet of Pleistocene crossbills.) Pine seeds are eaten only rarely today by *L. l. leucoptera*, thus the evolution of *L. megaplaga* likely involved a major shift in food habits, not unlike that seen in crossbills on the Mediterranean island of Mallorca versus those on the European continent (48). Such shifts in food habits might help to explain the low SDM climatic suitability scores of crossbills on the North American mainland versus those of the extirpated population in the Bahamas. Parchman et al. (29)

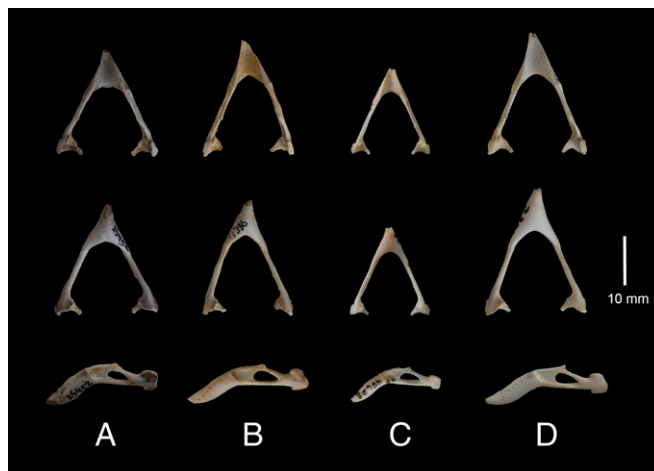


Fig. 5. Fossil and modern mandibles of crossbills (*Loxia*) in dorsal (Top row), ventral (Middle row), and lateral (Bottom row) aspects. (A) *L. megaplaga* modern, AMNH 25452, Dominican Republic. (B) *L. megaplaga* fossil, UF 297336, Abaco, Bahamas. (C) *L. l. leucoptera* modern UF 45638, Florida. (D) *L. curvirostra stricklandi* modern, UF 33216, Chiapas, Mexico.

Table 2. Comparative osteology of *Loxia*

Character	<i>L. curvirostra</i> modern	<i>L. l. leucoptera</i> modern	<i>L. megaplaga</i> modern	<i>L. megaplaga</i> Haiti fossils	<i>L. megaplaga</i> Abaco fossils
ROSTRUM					
Supranasal bar	Wide, flat	Narrow, ridged	Wide, flat	Wide, flat	—
Dorsal midline, anterior to nares	Smoothly rounded	Ridged	Ridged	Ridged	—
Median neurovascular sulcus	Shallow, poorly defined	Deep, distinct	Deep, distinct	Deep, distinct	—
Tomial margin in ventral aspect	Slightly concave	Highly concave	Highly concave	Highly concave	—
MANDIBLE					
Posterior extension of medial cotyla	Present	Absent	Absent	—	Intermediate
Relative length of cotyla lateralis	Short	Intermediate	Long	—	Long
Medial and lateral concavity of ramus just posterior to dentary	Shallow	Intermediate	Deep	—	Deep
NOTARIUM					
Number of fused thoracic vertebrae	3	2	3	—	—

suggested that coevolution with *L. megaplaga* led to the thicker cone scales in *P. occidentalis*. In the ice-age Bahamas, *L. megaplaga* presumably fed on the seeds of *P. caribaea* var. *bahamensis*, which are protected by somewhat thinner cone scales than in *P. occidentalis*. Speculation about possible coevolution awaits further research.

Conclusions

We propose that bluebirds and crossbills probably colonized the Bahamas sometime during the last glacial interval (i.e., subsequent to MIS 5e; <125 ka), when habitat conditions would have been more favorable than during the interglacial MIS 5e. Going from glacial (MIS 2) to interglacial (MIS 1) conditions during the PHT (~15–9 ka; cool → warm; dry → moist; large island → small island; near island → more isolated island; pine woodland and grassland → pine forest and broadleaf forest) would have depleted many of the pine grassland-dependent species of birds. Whether from glacial to interglacial or vice versa, each major shift in climate/sea level/habitat would cause some reshuffling of the resident Bahamian flora and fauna. Unlike on Bermuda, we currently lack a pre-LGM fossil record of Bahamian vertebrates, so the differences through time in this “reshuffling” (new colonizations, new extirpations) are speculative at this point. Developing a pre-LGM fossil record in the Bahamas is a major research challenge for the future.

Scientists agree nowadays that global temperatures are rising, as are sea levels (49). While these changes may not be as dramatic in magnitude as those that took place at the Pleistocene–Holocene Transition from ~15–9 ka, they are occurring rapidly and still are likely to contribute to floral and faunal changes on islands. This is especially the case because of the highly variable and often poorly understood effects that novel (= indigenous + introduced species) plant and animal communities will have on island ecosystems (50). The changes in climate, sea level, habitat, etc. brought on by the PHT rearranged insular biotic communities without any human influence. Today, these types of changes are exacerbated by all manner of human impacts.

Materials and Methods

Comparative osteology was done with modern skeletons from the American Museum of Natural History, Carnegie Museum of Natural History, Delaware Museum of Natural History, Los Angeles County Museum, Minnesota Museum of Natural History, Moore Laboratory of Zoology, Occidental College, Museum of Southwest Biology, University of New Mexico, Museum of Vertebrate Zoology, University of California, Berkeley, Florida Museum of Natural History, University of Florida (UF), National Museum of Natural History, Smithsonian Institution, and the Yale Peabody Museum (SI Appendix, Table S6). All fossils are from the UF Vertebrate Paleontology Collection, on long-term loan from the National Museum of the Bahamas.

The *Loxia* fossils are UF 297336–297342. The *Sialia* fossils are UF 312822–312824, 411423–411455.

We compared cones and seeds of *P. caribaea* var. *bahamensis* from the Bahamas to published measurements of *P. occidentalis* from Hispaniola, based on the proposal of coevolution in size between the cones of *P. occidentalis* and the bill of *L. megaplaga* (29). Using similar sampling methods that those authors used for *P. occidentalis* on Hispaniola, we measured cones and seeds for *P. caribaea* var. *bahamensis* from Abaco (SI Appendix, Table S5). We took the following measurements from two cones per cones collected from 23 different trees from eight locations on Abaco: cone length (in millimeters); cone width (in millimeters); cone mass (in grams); scale length and scale thickness (in millimeters) three scales per cone from middle third of cone (from each of the cones with seeds); seed mass (in milligrams) for all seeds filled with kernel (from any cone).

To evaluate the fluctuating land area in the Bahamian Archipelago for the past 492,000 y, spanning MIS 12 to the present, we use the sea level curve from Grant et al. (51). Sea level relative to present, at increments of 1,000 y, was applied to a global topographic database that includes seafloor topography (52) to estimate land area above sea level, at each time step, as in Steadman and Franklin (6) (for details see SI Appendix).

Species distribution modeling (53) was used to estimate the relative likelihood (54) of climatically suitable conditions in the current and ice age Bahamas for extant subspecies of *S. sialis*, *L. curvirostra*, and *L. leucoptera* (in North America only). Occurrence data were combined for some geographically adjacent subspecies that had small sample sizes (SI Appendix, Table S2). Occurrence data were obtained from the Global Biodiversity Information Facility, restricted to vouchered and research grade records, and six bioclimatic variables (55) were analyzed: annual temperature,

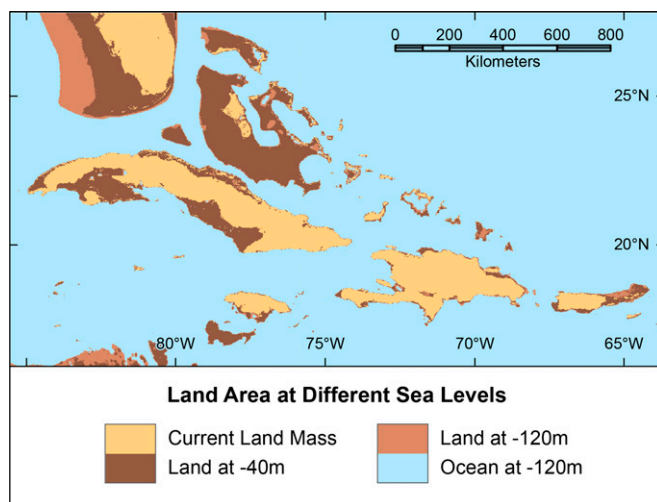


Fig. 6. Changing sea-level and extent of Caribbean islands through time. Modified from SI Appendix, Fig. S4 of ref. 6.

temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, and precipitation seasonality. Bioclimatic data for current climate and Last Glacial Maximum based on three paleoclimate models were obtained from www.worldclim.org at 2.5° resolution. Climate data and modeling procedures using MaxEnt software (56, 57) were as in Steadman et al. (5) and see *SI Appendix*. Averaged (and summed) climatic suitability (relative likelihood) predicted from SDMs, projected to current climate and hindcast to the LGM paleoclimate maps for Bahamas (including land areas exposed by lower sea level), were used to evaluate the degree of similarity between climate currently occupied by these populations and the current and ice age Bahamas climate.

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- Martin PS, Steadman DW (1999) Prehistoric extinctions on islands and continents. *Extinctions in Near Time: Causes, Contexts and Consequences*, ed MacPhee RDE (Kluwer Academic/Plenum Publishers, New York), pp 17–55.
- MacPhee RDE, Iturralde-Vinent MA, Jiménez Vázquez O (2007) Prehistoric sloth extinctions in Cuba: Implications of a new “last” appearance date. *Caribb J Sci* 43:94–98.
- Steadman DW, et al. (2014) Late Holocene faunal and landscape change in the Bahamas. *Holocene* 24:220–223.
- Soto-Centeno JA, Steadman DW (2015) Fossils reject climate change as the cause of extinction of Caribbean bats. *Sci Rep* 5:7971.
- Steadman DW, et al. (2015) Vertebrate community on an ice-age Caribbean island. *Proc Natl Acad Sci USA* 112:E5963–E5971.
- Steadman DW, Franklin J (2015) Changes in an insular bird community since the late Pleistocene. *J Biogeogr* 42:426–438.
- Hearty PJ, Kindler P, Cheng H, Edwards R (1999) A +20 m middle Pleistocene sea-level highstand (Bermuda and the Bahamas) due to partial collapse of Antarctic ice. *Geology* 27:375–378.
- Bowen D (2010) Sea level ~400 000 years ago (MIS 11): Analogue for present and future sea-level? *Clim Past* 6:19–29.
- Muhs DR, Pandolfi JM, Simmons KR, Schumann RR (2012) Sea-level history of past interglacial periods from uranium-series dating of corals, Curaçao, Leeward Antilles islands. *Quat Res* 78:157–169.
- Raymo ME, Mitrovica JX (2012) Collapse of polar ice sheets during the stage 11 interglacial. *Nature* 483:453–456.
- Chen J, Curran H, White B, Wasserburg G (1991) Precise chronology of the last interglacial period: ²³⁴U–²³⁰Th data from fossil coral reefs in the Bahamas. *Geol Soc Am Bull* 103:82–97.
- Thompson WG, Curran HA, Wilson MA, White B (2011) Sea-level oscillations during the last interglacial highstand recorded by Bahamas corals. *Nat Geosci* 4:684–687.
- Hearty PJ, Neumann AC, Kaufman DS (1998) Chevron ridges and runup deposits in the Bahamas from storms late in oxygen-isotope substage 5e. *Quat Res* 50:309–322.
- Avery JD, Fonseca DM, Campagne P, Lockwood JL (2013) Cryptic introductions and the interpretation of island biodiversity. *Mol Ecol* 22:2313–2324.
- White AW (1998) *A Birder's Guide to the Bahama Islands (Including Turks and Caicos)* (American Birding Association, Colorado Springs, CO).
- Raffaele HA, Wiley J, Garrido O, Keith A, Raffaele J (1998) *A Guide to the Birds of the West Indies* (Princeton Univ Press, Princeton).
- Bond J (1972) *Seventeenth Supplement to the Check-List of Birds of the West Indies* (Academy of Natural Sciences, Philadelphia).
- Pinkowski BC (1977) Foraging behavior of the Eastern Bluebird. *Wilson Bull* 89:404–414.
- Gowaty PA, Plissner JH (1998) Eastern Bluebird (*Sialia sialis*). *The Birds of North America* (The Birds of North America, Inc., Philadelphia), p 32.
- Corbin CE, Lowenberger LK, Dorkoski RP (2013) The skeleton flight apparatus of North American bluebirds (*Sialia*): Phylogenetic thrushes or functional flycatchers? *J Morphol* 274:909–917.
- Latta SC, Sondreal ML, Brown CR (2000) A hierarchical analysis of nesting and foraging habitat for the conservation of the Hispaniolan white-winged crossbill (*Loxia leucoptera megaplaga*). *Biol Conserv* 96:139–150.
- Latta SC, Sondreal ML, Mejia DA (2002) Breeding behavior of the endangered Hispaniolan Crossbill (*Loxia megaplaga*). *Ornitol Neotrop* 13:225–234.
- Benkman CW (1994) Comments on the ecology and status of the Hispaniolan Crossbill (*Loxia leucoptera megaplaga*), with recommendations for its conservation. *Caribb J Sci* 30:250–254.
- Riley JH (1916) *Three Remarkable New Species of Birds from Santo Domingo* (Smithsonian Institution, Washington, DC).
- Benkman CW (1992) *White-Winged Crossbill: Loxia leucoptera* (American Ornithologists' Union, Chicago).
- Bond J (1936) *Birds of the West Indies* (Academy of Natural Sciences, Philadelphia).
- Wetmore A, Swales BH (1931) The birds of Haiti and the Dominican Republic. *Bulletin US National Museum* 155:1–483.
- Parchman TL, Benkman CW, Britch SC (2006) Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*). *Mol Ecol* 15:1873–1887.
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- Parchman TL, Benkman CW, Mezquida ET (2007) Coevolution between Hispaniolan crossbills and pine: Does more time allow for greater phenotypic escalation at lower latitude? *Evolution* 61:2142–2153.
- Varela S, Lobo JM, Hortal J (2011) Using species distribution models in paleobiogeography: A matter of data, predictors and concepts. *Palaeogeogr Palaeoclimatol Palaeoecol* 310:451–463.
- Franklin J, Potts AJ, Fisher EC, Cowling RM, Marean CW (2015) Paleodistribution modeling in archaeology and paleoanthropology. *Quat Sci Rev* 110:1–14.
- Wright NA, Steadman DW (2012) Insular avian adaptations on two Neotropical continental islands. *J Biogeogr* 39:1891–1899.
- Wright NA, Steadman DW, Witt CC (2016) Predictable evolution toward flightlessness in volant island birds. *Proc Natl Acad Sci USA* 113:4765–4770.
- James HF (2009) Repeated evolution of fused thoracic vertebrae in songbirds. *Auk* 126:862–872.
- Howell SNG, Webb S (1998) *A Guide to the Birds of Mexico and Northern Central America* (Oxford Univ Press, Oxford, UK).
- Adkisson CS (1996) *Red Crossbill: Loxia curvirostra* (American Ornithologists' Union, Chicago).
- Carew JL, Myroie JE (1995) Quaternary tectonic stability of the Bahamian Archipelago: Evidence from fossil coral reefs and flank margin caves. *Quat Sci Rev* 14:145–153.
- Clark PU, et al. (2009) The last glacial maximum. *Science* 325:710–714.
- Denton GH, et al. (2010) The last glacial termination. *Science* 328:1652–1656.
- Jackson ST, et al. (2000) Vegetation and environment in eastern North America during the last glacial maximum. *Quat Sci Rev* 19:489–508.
- Peterson LC, Haug GH, Hughen KA, Röhl U (2000) Rapid changes in the hydrologic cycle of the tropical Atlantic during the last glacial. *Science* 290:1947–1951.
- Oswald JA, Steadman DW (2011) Late Pleistocene passerine birds from Sonora, Mexico. *Palaeogeogr Palaeoclimatol Palaeoecol* 301:56–63.
- Oswald JA, Steadman DW (2015) The changing diversity and distribution of dry forest passerine birds in northwestern Peru since the last ice age. *Auk* 132:836–862.
- Steadman DW, Oswald JA, Rincón AD (2015) The diversity and biogeography of late Pleistocene birds from the lowland Neotropics. *Quat Res* 83:555–564.
- Olson SL, Hearty PJ (2003) Probable extirpation of a breeding colony of Short-tailed Albatross (*Phoebastria albatrus*) on Bermuda by Pleistocene sea-level rise. *Proc Natl Acad Sci USA* 100:12825–12829.
- Olson SL, Wingate DB, Hearty PJ, Grady FV (2005) Prodrum of vertebrate paleontology and geochronology of Bermuda. *Proceedings of the International Symposium "Insular Vertebrate Evolution: The Palaeontological Approach."* *Monog Societat d'Història Natural de les Balears*, eds Alcover JA, Bover P (Editorial Moll, Mallorca, Spain), Vol 12, pp 219–232.
- Olson SL, Hearty PJ, Pregill GK (2006) Geological constraints on evolution and survival in endemic reptiles on Bermuda. *J Herpetol* 40:394–398.
- Björklund M, Alonso D, Edelaar P (2013) The genetic structure of crossbills suggests rapid diversification with little niche conservatism. *Biol J Linn Soc Lond* 109:908–922.
- Intergovernmental Panel on Climate Change (2014) *Climate Change 2014—Impacts, Adaptation and Vulnerability: Regional Aspects* (Cambridge Univ Press, Cambridge, UK).
- Lugo AE, Carlo T, Wunderle J (2012) Natural mixing of species: Novel plant–animal communities on Caribbean islands. *Anim Conserv* 15:233–241.
- Grant KM, et al. (2014) Sea-level variability over five glacial cycles. *Nat Commun* 5:5076.
- Smith WHF, Sandwell DT (1997) Global sea floor topography from satellite altimetry and ship depth soundings. *Science* 277:1956–1962.
- Franklin J (2010) *Mapping Species Distributions: Spatial Inference and Prediction* (Cambridge Univ Press, Cambridge, UK), pp 1–320.
- Guillera-Arroita G, et al. (2015) Is my species distribution model fit for purpose? Matching data and models to applications. *Glob Ecol Biogeogr* 24:276–292.
- Williams KJ, Belbin L, Austin MP, Stein JL, Ferrier S (2012) Which environmental variables should I use in my biodiversity model? *Int J Geogr Inf Sci* 26:2009–2047.
- Elith J, et al. (2011) A statistical explanation of MaxEnt for ecologists. *Divers Distrib* 17:43–57.
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecol Modell* 190:231–259.