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Global Ecology and Biogeography

RESEARCH PAPER

Global patterns of connectivity and isolation of populations of forest bird species in the late Pleistocene

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ABSTRACT

Aim Species' distributional responses to cool periods in the Pleistocene appear to have been diverse, but patterns of response are poorly known globally, and the nature of distributional responses to interglacial conditions remains largely unknown. The aim of this contribution is to assess distributional responses of forest bird species to Last Interglacial (LIG) and Last Glacial Maximum (LGM) conditions within nine forest regions world-wide, to test whether different regions experienced consistently different types of distributional responses.

Location Global.

Methods We use ecological niche modelling approaches under an assumption of ecological niche conservatism to assess degrees of fragmentation of species distributions through the LIG–LGM–present transitions. Models trained under present-day conditions were transferred to Pleistocene conditions, and fragmentation of potential distributional areas was assessed using FragStats.

Results Our results showed four regions to have greater fragmentation at LGM than at LIG or at present; three showed greater connectivity at LGM; and two were equivocal.

Main conclusions Our results suggest that the world is a patchwork of regions in which forest species experienced either consistently greater or consistently lesser population subdivision during the alternating cool and warm periods that characterized the Pleistocene. Speciation timing and dynamics should differ dramatically among major regions and biomes if these periods of connection and disjunction translate into speciation opportunity.

Keywords

Biogeography, forest bird, Last Glacial Maximum, Last Interglacial, Pleistocene, speciation, species distributions.

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INTRODUCTION

Understanding of the ecology, geography and history of biological diversity has broadened and gained significant additional detail, thanks to several new approaches and data streams. In particular, molecular sequence data and associated coalescent analyses provide insight into recent population history (Knowles, 2006), and ecological niche modelling techniques offer views into potential past geography (Peterson & Nyári, 2007; Nogués-Bravo, 2009). These approaches have permitted novel views of the biogeographic history of species and communities (Knowles, 2004; Knowles *et al.*, 2007; Araújo *et al.*, 2008; Nogués-Bravo *et al.*, 2010; Nyári *et al.*, 2010).

A focus of considerable discussion and debate has been the role of Pleistocene climatic fluctuations in the generation of modern biological diversity (Haffer, 1974; Bush, 1994; Zink & Slowinski, 1995; Bonaccorso *et al.*, 2006; Moyle *et al.*, 2009). The Pleistocene is either the period in which much of the present biodiversity was generated, or a period in which biodiversity generated *earlier* had to respond to dramatically changing conditions (Klicka & Zink, 1997; Avise & Walker, 1998; Bennett, 2004; Johnson & Cicero, 2004; Weir & Schluter, 2004; McCormack *et al.*, 2011). As the debate has raged in a lively fashion, some perhaps more pertinent aspects of Pleistocene biogeography have fallen by the wayside – in particular, a general understanding of the varied types of effects of climatic shifts on the distribution of species (Lomolino *et al.*, 2005; Peterson, 2009).
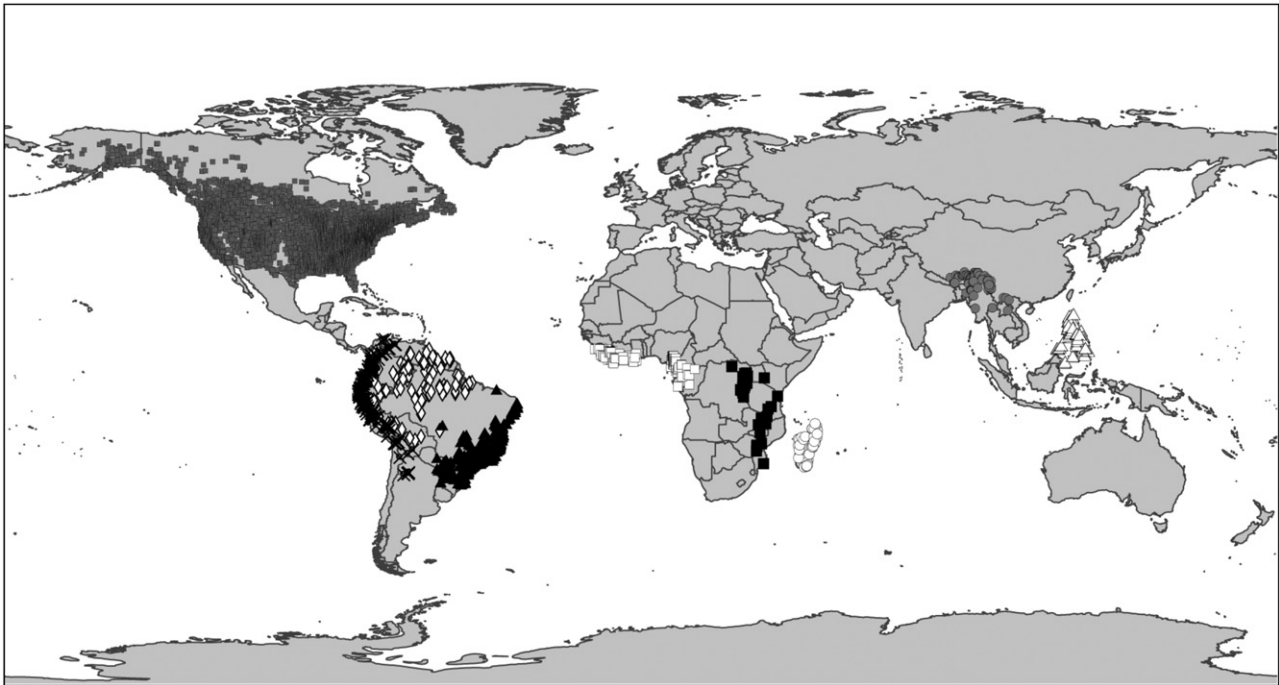
Figure 1 Geographic distribution of regions analysed in this paper, shown as occurrence points for the species analysed in each region, including North America (grey squares), Andes (black ×), Amazon Basin (white diamonds), Atlantic Forest (black triangles), west Africa (white squares), east Africa (black squares), Madagascar (white circles), east and south Asia (grey circles), and the Philippines (white triangles).

The debate has been reduced to simple orders of magnitude of timing (i.e. *c.* 10^5 to *c.* 10^6 years versus considerably older), rather than focusing on the details of geography and environments that may be more of interest.

For example, what are the ways in which species ranges in North America responded to the warm and cool cycles of the Pleistocene? Major known distributional responses include: (1) simple southward range contraction followed by northern expansion after the retreat of the glaciers, (2) range contraction and persistence of species in small refugial pockets of former ranges, (3) range fragmentation into larger (but isolated) refugia, (4) range expansion to form a broader and more continuous range, and (5) relative geographic stasis. While examples of each of these responses are known for North America (Mengel, 1970; Lanner & van Devender, 1981; Thompson & Anderson, 2000; Davis & Shaw, 2001; Lyons, 2003; Peterson *et al.*, 2004), the global response pattern is less well characterized, and dynamics of species ranges through glacial and interglacial periods are particularly poorly known.

In this paper we explore one important dimension of global Pleistocene biogeography: the relative effects of warm and cool periods on population fragmentation and possible speciation of forest birds. Although forest birds provided an important early body of evidence in the Pleistocene speciation debate (Haffer, 1974; Simpson & Haffer, 2003), decades of subsequent research attention have failed to produce a consensus in the field. We consider this debate to be overly simplified; here, instead, we

examine whether different world regions and biomes experienced different classes of responses to Pleistocene climatic changes based on projected responses of individual species, thus approaching the question from a perspective distinct from that of other recent studies (Harrison & Prentice, 2003). We reflect on implications of this analysis for understanding speciation and biological diversification.

METHODS

Input data

Occurrence data for 58 forest bird species in nine world regions were obtained thanks in large part to the kind collaboration of BirdLife International (see Acknowledgements; only records accorded locality certainty scores of 'certain' were used; Fig. 1). The two exceptions with regard to occurrence data sources were North America, for which occurrence data were drawn from the North American Breeding Bird Survey (Sauer *et al.*, 2001), and the Amazon Basin, for which we drew occurrence data from a previous analysis, itself based on data associated with vouchered museum specimens (Bonaccorso *et al.*, 2006). Species were generally chosen on the basis of data availability, except for North America, where we chose species at random from a much larger suite of forest bird species. Sample sizes ranged from 6 to 2911 unique occurrence localities per species (see Appendix S1 in

Supporting Information for a summary of species and sample sizes).

Climate data for the present day were drawn from the WorldClim climate archive (Hijmans *et al.*, 2005), which is parallel to the more familiar New *et al.* (1999) data set, but more immediately applicable to biological questions thanks to the 'bioclimatic variables' that it includes. In particular, to represent overall tendencies and variation in temperature and precipitation, we used a subset of the 'bioclimatic' coverages: annual mean temperature, mean diurnal temperature range, maximum temperature of the warmest month, minimum temperature of the coldest month, annual total precipitation, and precipitation of the wettest and driest months. This subset of the 19 original bioclimatic datasets was chosen based on assessment of the Pearson product–moment correlations among variables, eliminating one variable from each pair that shows high correlation coefficients (Jiménez-Valverde *et al.*, 2009). All analyses were developed at a spatial resolution of 2.5′ (*c.* 5 km at the Equator), reflecting the approximate spatial accuracy of the georeferencing; analyses were developed within an area delimited by a buffer around known occurrence points of the group of species from a biome with a radius equal to the width of the largest disjunction between occurrence points within the biome, as a crude approximation of the area that has been accessible to the species over relevant periods of time, which is the appropriate area for model calibration (Barve *et al.*, 2011).

To summarize Pleistocene climates (LGM = Last Glacial Maximum, 20,000 yr BP; LIG = Last Interglacial, 135,000 yr BP) at the same spatial resolution as that of the present-day data, we used new, fine-resolution climate data sets recently developed by R. J. Hijmans (pers. comm.; see summary of methods below), to parallel the WorldClim current climate data. LGM data were drawn from the outputs of general circulation model (GCM) simulations from the Community Climate System Model (CCSM; Kiehl & Gent, 2004), downloaded from the website of the Paleoclimate Modelling Intercomparison Project 2 (http://www.pmip2.cnrs-gif.fr/). LIG data were based on simulations for that time period using the CCSM GCM (Otto-Bliesner *et al.*, 2006b), specifically the CCSM-3 Glacial Simulation (Otto-Bliesner *et al.*, 2006a).

The GCM data had a native spatial resolution of 2.8° (c. 300 km × 300 km at the Equator), which were downscaled via the following procedure. First, the difference between the GCM output for historical and recent conditions was calculated. These differences were then interpolated to a 2.5′-resolution grid using the spline function in ARCINFO (ESRI, Redlands, CA) with the tension option. The interpolated differences were then added to the high-resolution current climate data sets from WorldClim. Finally, established routines (http://www.worldclim.org/bioclim-aml) were used for generating the so-called 'bioclimatic' data sets from the raw monthly temperature and precipitation data. This procedure has the dual advantage of producing palaeoclimatic data sets at resolutions relevant to the spatial scale of analysis, and of calibrating the simulated climate change data to the actual observed (present-day) climate data.

Ecological niche modelling

We used the Genetic Algorithm for Rule-Set Prediction (GARP; Stockwell & Peters, 1999) and Maxent (Phillips *et al.*, 2006) for generating an initial suite of ecological niche models for each species. Some Maxent models, however, showed odd behaviour when thresholded – for example, broad lowland areas in the western Amazon Basin were included in present-day models for some Andean species. An example of this behaviour is shown in Appendix S2.

As a consequence, we used GARP throughout the rest of the analyses. GARP is an evolutionary-computing method that estimates ecological niches based on non-random associations between known occurrence points for species and sets of GIS coverages describing environmental dimensions of landscapes. Occurrence data are used by GARP as follows: 50% of occurrence data points are set aside for an independent test of model quality, and 50% are used for developing models. 'Pseudoabsence' points (i.e. pixels selected from the set of areas lacking known presences) are also sampled. In the end, two data sets are created, each of 1250 presence (resampled from whatever points are input for model calibration) and pseudoabsence points, which are used for rule generation and model testing, respectively (Stockwell & Peters, 1999).

Within GARP processing, a first rule is created by applying a method chosen randomly from a set of inferential tools (e.g. logistic regression, bioclimatic rules). The genetic algorithm consists of specially defined operators (e.g. crossover, mutation) that modify the initial rules; after each modification, the quality of the rule is tested (maximizing both significance and predictive accuracy) and a size-limited set of best rules is retained, so the resulting models have 'evolved'. Because rules are tested based on independent data (intrinsic test data), performance values reflect the expected performance of the rule, an independent verification that gives a more reliable estimate of true rule performance. The final result is a set of rules that can be projected onto a map to estimate a potential geographic distribution for the species under investigation or projected onto another landscape or time period, again to estimate a potential distribution under changed circumstances (Soberón & Peterson, 2005).

Following best-practice recommendations (Anderson *et al.*, 2003), we developed 100 replicate random-walk GARP models and filtered out 90% of the replicates based on consideration of error statistics, as follows. We applied an initial filter removing models that omit (omission error = predicting absence in areas of known presence) heavily, based on the extrinsic testing data, and a second filter based on an index of commission error (= predicting presence in areas of known absence), in which models predicting very large and very small areas are removed from consideration. Specifically, in Desktop GARP (Pereira, 2001), we used a relative omission threshold in which we retained the 20% of models with the lowest omission, and then retained the 50% of replicate models with commission indices closest to the median area predicted present; the result was 10 replicate binary model predictions that were summed to produce a best estimate of geographic prediction.

Model evaluation

Because ENMs must be tested for predictive ability prior to interpretation and exploration (Peterson, 2005), particularly for transferability challenges such as this one (Nogués-Bravo, 2009), we tested the predictive ability of models via a series of spatially stratified subsetting exercises (Peterson & Shaw, 2003). In particular, we tested the internal consistency of ecological niche characteristics for each species by means of separating the distribution of available occurrence data into three equal groups along the broad axis of the species distribution (e.g. for Andean species, subdivision was by latitude). For reasons of practicality, only species for which ≥ 50 occurrences were available were subjected to these tests; the two 'outer' thirds of the distribution were used to calibrate models that were then evaluated with the $c. \geq 17$ occurrences in the central region.

Within the testing area, we calculated the proportional area predicted present at each threshold of the GARP model, as well as the success in predicting each independent test point at each threshold. We did not employ the traditional receiver operating characteristic (ROC) analyses (Fielding & Bell, 1997), owing to concerns regarding emphases of such approaches that do not focus on prediction of the entire distributional area (Lobo *et al.*, 2008; Peterson *et al.*, 2008). Instead, we used a modification of the ROC approach (Peterson *et al.*, 2008), in which only a part of the overall ROC space is considered, depending on expected error levels in the input occurrence data – basically the proportion of records expected to be sufficiently inaccurate that they may fall artificially in areas of unsuitable conditions, termed E (Peterson *et al.*, 2008), and which we set at 0.05 for all tests. The partial ROC calculations, which involve bootstrapping the underlying data to test whether the empirical curve is significantly elevated above random expectations (Peterson *et al.*, 2008), were carried out using programs developed by N. Barve (pers. comm.; available from the senior author by request).

Projection to Pleistocene conditions

Once the predictive ability of models in the present day was confirmed, we developed a present-day model for each species based on all available occurrences for the species (i.e. without subsetting for evaluation). We used the same protocols for ENM development, but projected the resulting best-subsets models onto the LIG and LGM climatic coverage sets described above. The result was an estimate of Pleistocene suitability of landscapes for each taxon under analysis, based on the present-day ecological requirements of the species. This approach of palaeo-prediction has already seen considerable testing and exploration (Peterson & Nyári, 2007; Waltari *et al.*, 2007; Nogués-Bravo *et al.*, 2008; Nogués-Bravo, 2009; Waltari & Guralnick, 2009; Nyári *et al.*, 2010), in which its predictive power has been confirmed (but see Varela *et al.*, 2009).

Once present-day, LGM and LIG projections of niche models were in hand, we established appropriate thresholds for separating prediction of presence versus absence based on the least training presence threshold approach (Pearson *et al.*, 2007), but

modified to take into account the expected error parameter E (see above). That is, instead of setting a threshold at the value that includes 100% of the training occurrence data, we used the threshold that includes $(100–E)$% of the training occurrence data, which is thus a more restricted area but takes into account the possible presence of noise in the occurrence data. Thresholds were established based on the present-day models, and then applied to LIG and LGM maps as well.

Fragmentation

Finally, with thresholded model projections to the present day, LGM and LIG, we used FragStats version 3.3 to calculate three indices relevant to population fragmentation and subdivision (McGarigal *et al.*, 2002). These indices are as follows. COHESION is the Patch Cohesion Index, which measures the physical connectedness of the patches in a particular class, ranging from 0 (patches more subdivided) to 100 (patches completely connected and entire in shape). The formula is

$$\text{COHESION} = 100 \left(1 - \frac{\sum_{j=1}^{n} p_{ij}}{\sum_{j=1}^{n} p_{ij} \sqrt{a_{ij}}}\right)\left(1 - \frac{1}{\sqrt{A}}\right)^{-1},$$

where p_{ij} is the perimeter of patch ij in terms of number of cell surfaces, a_{ij} is the area of patch ij in terms of number of cells and A is the total number of cells in the landscape. CPLAND is the core area percentage of the landscape, which measures the relative coverage of the landscape by core areas of patches. The formula is

$$\text{CPLAND} = 100 \left(\frac{\sum_{j=1}^{n} a_{ij}^{c}}{A}\right),$$

where c indicates that areas refer to core areas as defined based on a specified edge depth of 0.1° and other variables are as defined above. Finally, NDCA counts the number of disjunct core areas (again based on an edge depth of 0.1°), calculated as

$$\text{NDCA} = \sum_{j=1}^{n} n_{ij}^{c},$$

where n_{ij}^{c} is the number of disjunct core areas in patch ij based on the specified edge depth. These three measures together summarize what are perhaps the most relevant dimensions of distributional area fragmentation from the perspective of population connectivity; they were calculated for each species for each time period.

RESULTS

Tests of the predictive ability of models affirmed that the models developed had an excellent ability to anticipate the distributions of species, even in regions for which no occurrence data were available during model development. That is, of 22 species for
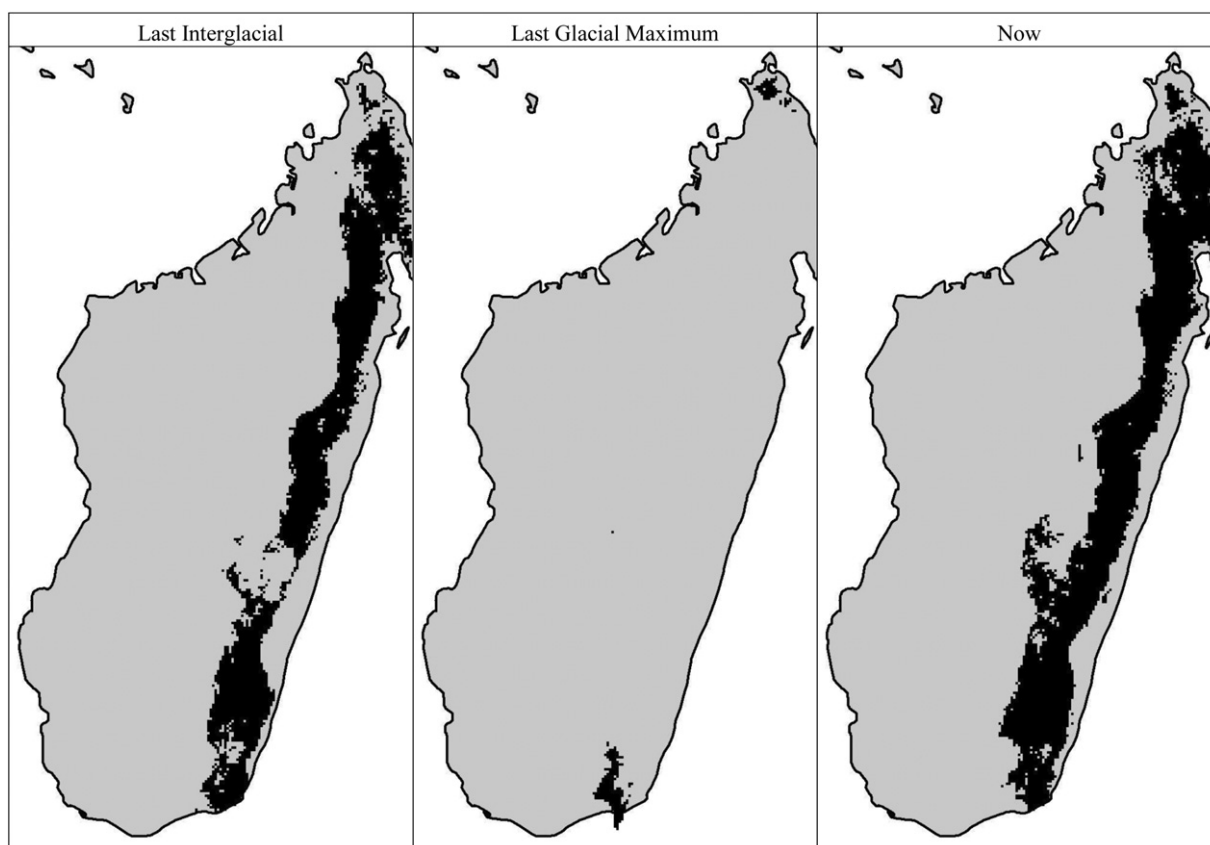
Figure 2 Example summary of likely potential distributional area of *Brachypteracias leptosomus* in the present day, Last Glacial Maximum (LGM, 20,000 ka) and Last Interglacial (135,000 ka), derived from ecological niche models based on present-day occurrences, with the assumption of no evolutionary change in ecological niche characteristics over the period of interest. Note that LGM predictions extend beyond current coastlines, reflecting lower global sea level at that point in time.

which sample sizes of occurrence data were ≥ 50, 19 predictions were highly statistically significantly better than random expectations – that is, in the partial ROC tests, all 19 predictions yielded ROC curves that were significantly elevated above null expectations ($P < 0.001$; Appendix S1). The three species for which model predictions were not statistically significant were *Automolus infuscatus* ($P = 0.103$), *Formicarius colma* ($P = 0.229$) and *Catharus guttatus* ($P = 0.053$) – model failure appeared to be a consequence of low statistical power resulting from the great bulk of the testing area being predicted as suitable. Overall, though, with this general demonstration of the predictive ability of the models we explored model projections onto palaeoclimate scenarios to estimate Pleistocene potential distributional areas of each species using all available occurrence data (i.e. without the spatial subsetting).

Projections onto palaeoclimate scenarios yielded diverse patterns of range configuration through time. In general, ranges reconstructed at the LIG were closely similar to present-day ranges, and LGM ranges were distinct and different in extent, shape and level of fragmentation (Figs 2–5; see Appendix S1). This result – in the simplest sense – is logical, given that LIG represents a period of relative warmth during the Pleistocene, much like present-day conditions, whereas the LGM was a

period of much cooler global climates, contrasting dramatically with the other two periods.

The direction of the differences between LGM and LIG/present ranges, however, varied among regions rather dramatically. In Madagascar, for example, *Brachypteracias leptosomus* was reconstructed as having a range that is currently rather continuous along the central-eastern north–south chain of mountains that dominate the island, and was reconstructed as similarly continuous at the LIG, but dramatically fragmented at the LGM (Fig. 2). Indeed, in two cases among birds from Madagascar this fragmentation was so extreme and the fragments so tiny that only one refugium was reconstructed at the LGM (a northern refugium in *Tyto soumagnei* and a southern refugium in *Newtonia fanovanae*). Similar LGM fragmentation of LIG/present-day continuous ranges was observed in the Amazon Basin (Fig. 3), West Africa and (to some degree) North America.

On the other hand, other regions present relatively fragmented ranges at present, and were reconstructed similarly at the LIG, but were more continuously distributed at the LGM. For example, in the guan *Aburria aburri*, the present-day and reconstructed LIG ranges are linear, with significant breaks (e.g. across the valley of the Apurimac River in southern Peru); at the LGM, however, this species was reconstructed as being able to colonize somewhat
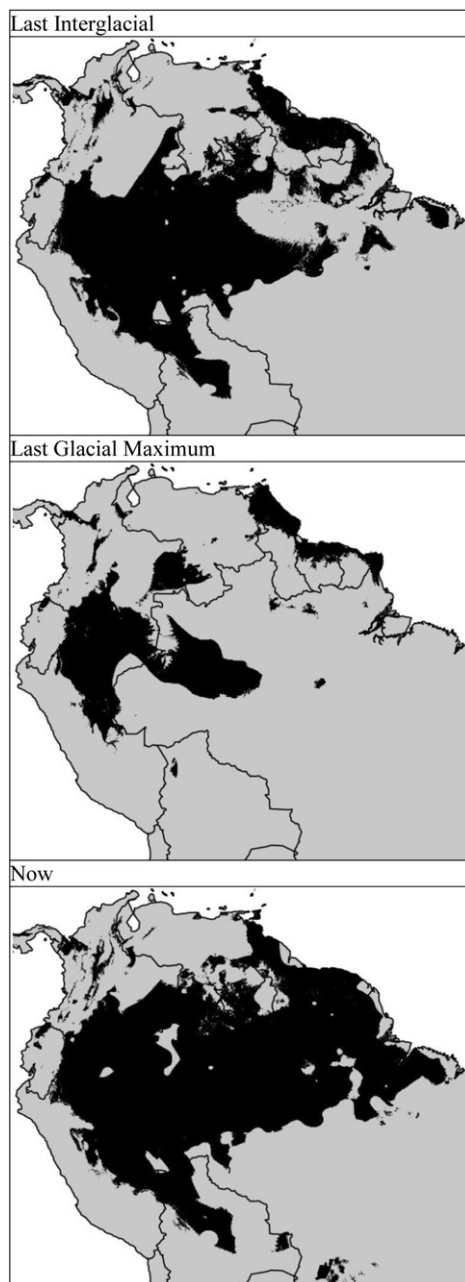
Figure 3 Example summary of likely potential distributional area of *Tangara mexicana* in the present day, Last Glacial Maximum (20,000 ka) and Last Interglacial (135,000 ka), derived from ecological niche models based on present-day occurrences, with the assumption of no evolutionary change in ecological niche characteristics over the period of interest.

lower-elevation areas east of the Andes, creating a near-continuous distributional area along the length of the Andean Cordillera (Fig. 4). Similar continuous LGM reconstructions were derived from the Philippines (Fig. 5) and East Africa.

These contrasting patterns were summarized in terms of range cohesion and fragmentation metrics by comparing the LGM reconstruction with LIG and present-day reconstructions (Table 1, Fig. 6). Here, four regions showed minimum values for

COHESION, CPLAND and NDCA at the LGM (Madagascar, Amazon Basin, North America and West Africa), indicating greater population fragmentation at the LGM. Three other regions showed maximum values of those same indices at the LGM (Andes, East Africa, Philippines), indicating greater population connectivity at the LGM. Two regions (the Himalayas and the Atlantic Forest) showed more equivocal patterns – either dominated by intermediate values (Himalayas) or balanced between LGM-fragmented and LGM-connected signatures (Atlantic Forest). We note that values of COHESION generally show only quite subtle differences in values (Appendix S1); regardless, the patterns we note are manifested in the other two indices.

DISCUSSION

Caveats

The validity of the niche palaeoprojection approach depends rather critically on the conservatism of ecological niche characters over 135,000 years of evolutionary time (Nogués-Bravo, 2009). Although concerns in this study are assuaged to some degree by the indication that niches have not diverged dramatically across the network of populations that make up species' ranges (Appendix S1), the assumption of niche conservatism must be borne in mind as underlying the results of this study. A recent review of the available evidence on this point confirmed rather broadly that ecological niche conservatism is a very general pattern (Peterson, 2011), suggesting that this assumption may be acceptable.

A similar concern regards the stability of the local-to-regional correlation structure of climates over the 135,000 years covered by our projections. That is, we use current, fine-scale associations between features of climates to downscale GCM results from relatively coarse (2.8°) to relatively fine (2.5′). However, if these associations were not to prove stable over the end of the Pleistocene and into the present day, then this downscaling procedure would not be robust. Concerns centre on sub-grid scale topography and how it modulates the surface fields; however, reducing the differential between original and downscaled versions would affect the fragmentation indices on which this study is based in unknown ways. WorldClim provides the primary climatic baseline, which was adjusted for each time slice according to the anomalies in the GCM-predicted climate, and as such accounts for topographic features, so the assumption that at least the first-order structures of the surface fields are reasonably realistic is probably safe. In the future, however, it will become possible to use high-resolution regional models (i.e. at the same or higher resolution as the WorldClim data) nested within the global models (Rummukainen, 2010) to provide the climatic information directly, without the need for a downscaling step.

More biologically, a further caveat is that our climate data sets take into account climate variability only in a quite indirect fashion – if patterns of variability in climate features were to differ markedly between the present day and the LIG and LGM, these differences could further compromise our results, requir-
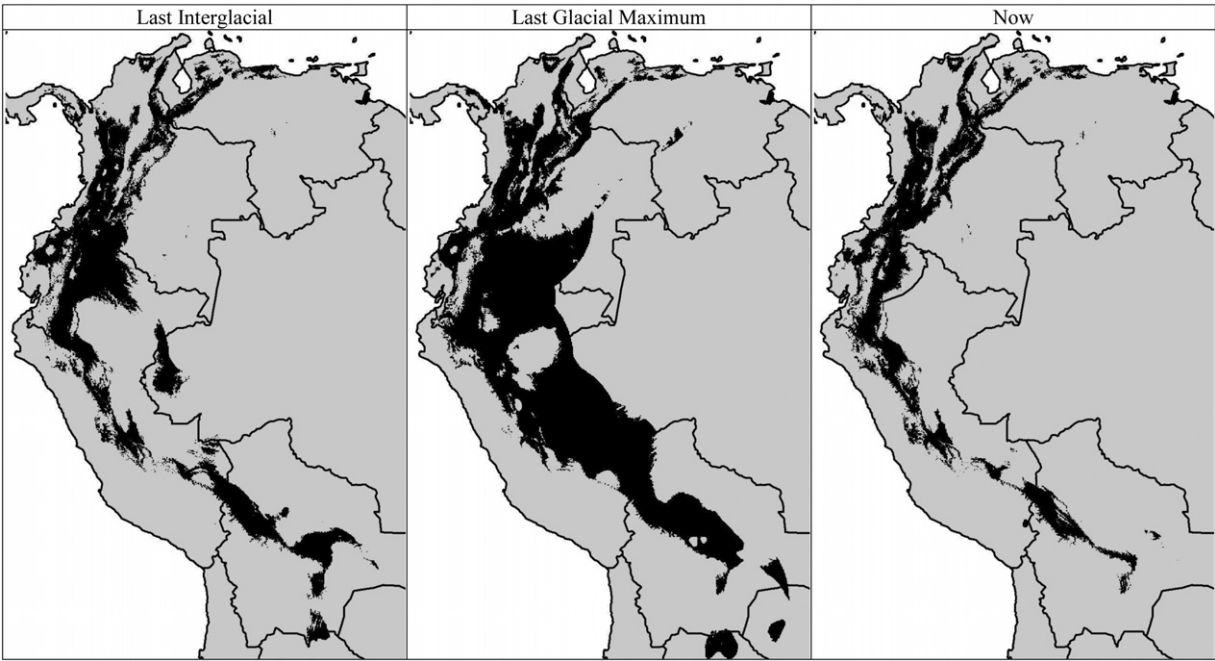
Figure 4 Example summary of likely potential distributional area of *Aburria aburri* in the present day, Last Glacial Maximum (20,000 ka), and Last Interglacial (135,000 ka), derived from ecological niche models based on present-day occurrences, with the assumption of no evolutionary change in ecological niche characteristics over the period of interest.

Figure 5 Example summary of likely potential distributional area of *Ducula carola* in the present day, Last Glacial Maximum (LGM, 20,000 ka) and Last Interglacial (135,000 ka), derived from ecological niche models based on present-day occurrences, with the assumption of no evolutionary change in ecological nic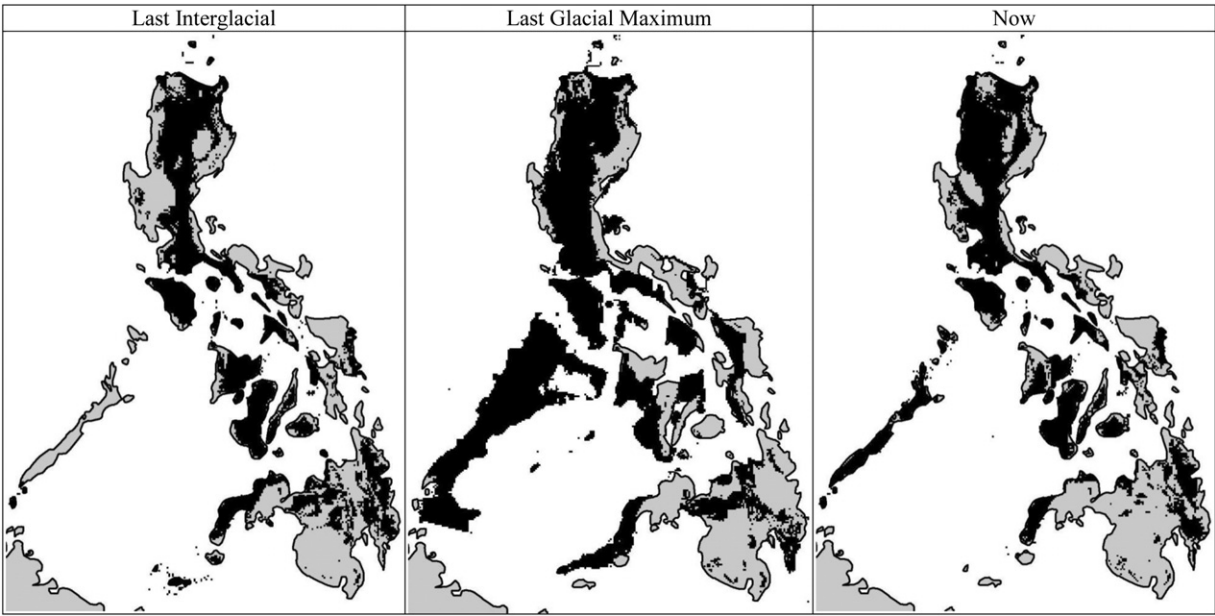he characteristics over the period of interest. Note that LGM predictions extend beyond current coastlines, reflecting lower global sea level and connectivity between present-day islands at that point in time.

ing more detailed studies of fully coupled climate data (e.g. through nested regional models), in which the details of such variability are considered more explicitly. The palaeoprojection approach also assumes – at least as regards the details, if not the general points – that climatic changes are not so fast that species are unable to establish distributional equilibrium, which may be a relatively slow process (Svenning & Skov, 2004, 2007; Svenning *et al.*, 2008).

Table 1 Summary of trends between the Last Interglacial, Last Glacial Maximum (LGM) and the present day, in terms of the patch cohesion index (COHESION), core area percentage of the landscape (CPLAND), and number of disjunct core areas (NDCA), all indices of fragmentation of populations across the species' distributional area. Presentation is in terms of whether the LGM value for a particular species is the lowest of the three values (Min), the highest of the three (Max), or intermediate (Int).

| Region	COHESION			CPLAND			NDCA			LGM state
	Min	Int	Max	Min	Int	Max	Min	Int	Max	
Amazon Basin	4	0	2	6	0	0	6	0	0	Fragmented
Andes	2	0	4	2	1	3	1	4	1	Connected
Atlantic Forest	6	0	6	9	1	2	6	0	6	Equivocal
East Africa	1	1	3	2	0	3	2	2	1	Connected
Himalayas	2	1	0	0	2	1	0	3	0	Equivocal
Madagascar	3	1	1	5	0	0	4	1	0	Fragmented
North America	7	2	0	8	1	0	9	0	0	Fragmented
Philippines	1	0	6	1	1	5	2	2	3	Connected
West Africa	5	1	0	5	1	0	4	2	0	Fragmented
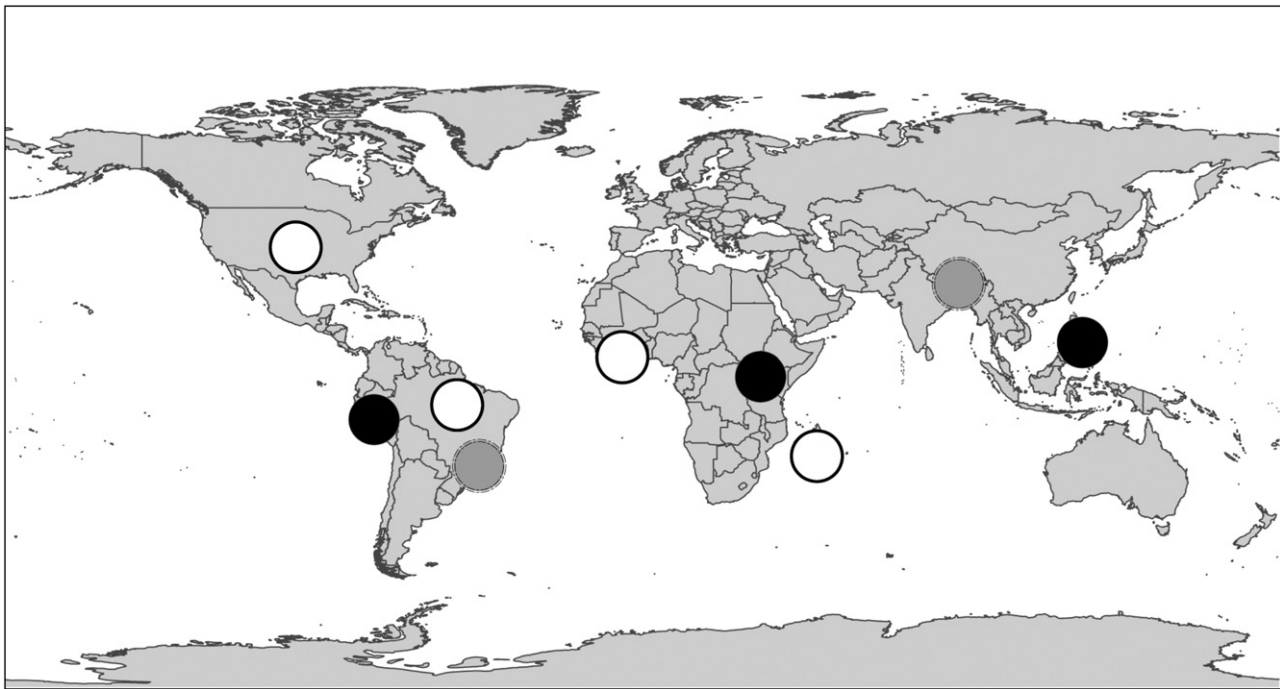
Figure 6 Summary of results regarding timing of periods of relative connectivity versus periods of relative isolation of populations of forest birds in nine world regions. White indicates areas where isolation and speciation probably occurred in global cool periods, black indicates areas where isolation and speciation probably occurred in global warm periods and grey areas were equivocal.

Finally, as discussed above (Results), we are concerned about the relatively subtle numerical differences among time periods, particularly in the COHESION metric. That is, the numbers presented in the Appendix S1 are quite similar in many cases for that metric. COHESION is related monotonically to the proportion of the landscape covered by a species' distribution, and for that reason the metric may be relatively insensitive to range-margin fluctuations or appearance of narrow barriers within the species' range, but these points do merit some concern. However, the maps per se do show very real, macrogeographic shifts that are visually indicative of changes in degree of fragmentation; the other two fragmentation metrics are less subtle; and the albeit subtle variation in COHESION nonetheless shows consistent differences among time periods in some regions. For these reasons, we interpret these results as we have.

Implications

The present study uses a new progression of steps for understanding and reconstructing the geography of species in response to changing climates. Rather than focus on patterns manifested in particular species, we have used forest-dwelling bird species as an aggregate set or 'probe' to establish what more general effects were likely to be affecting broader groups (classes or guilds) of forest species. The result – that different regions experienced fragmentation (and possible speciation opportunities) differently in cold versus warm periods – may appear at first glance to be as expected. Indeed, most investigators in the field would probably have predicted this result, at least for a few regions, without analyses and quantitative approaches.

The point, however, is more subtle and interesting than it may appear at first glance. Adjacent biomes were likely to be experiencing 'fragmentation' phases versus 'connection' phases in alternate time periods – ideal examples would be the Andes as compared with the Amazon, East Africa as compared with West Africa, etc. These contrasts imply that speciation (or at least the most recent event of population subdivision and isolation) in the LGM-connected species would have occurred farther back in time (LIG) than for the LGM-fragmented species, i.e. sister species pairs in the Andes should be older than sister species pairs in the Amazon. Minimally, these results suggest that speciation would have occurred at *different* points in time in the different regions (Fig. 6), and these temporal offsets may have been repeated, according to the oscillations throughout the Pleistocene. This hypothesis is eminently testable as increasing numbers of clades are analysed in terms of time-calibrated molecular phylogeography and phylogeny (provided, of course, that the time calibration is done carefully and responsibly; Peterson, 2007).

These results also have implications regarding deeper-time speciation geography, which has been the focus of considerable debate in recent decades (Klicka & Zink, 1997; e.g. Johnson & Cicero, 2004). The crux of these discussions has been that of relative timing – whether splits between sister species pairs date to the Pleistocene (10^5–10^6 Ma) or are deeper (e.g. to the Pliocene, which would be appreciably older than 10^6 Ma) – which has been assessed via molecular clock approaches. Approaches to dating phylogenetic splits have sparked considerable controversy, which in itself reduces confidence in such arguments (Ho & Larson, 2006; Peterson, 2007), although more robust techniques are being explored (McCormack *et al.*, 2011).

The results of this study offer an immediate means by which to enrich and inform this argument. That is, the question is not one of just timing, but also of whether conditions at those times were appropriate for speciation to occur. If the Pleistocene (10^5–10^6 Ma) was as cool as or much cooler than present-day conditions, and if the Pliocene [$(2$–$5) \times 10^6$ Ma] saw markedly *warmer* climates (Salzmann *et al.*, 2009), then general Pliocene connectivity of populations should probably resemble that of the present day, only in a more exaggerated way, and not that of the globally cool periods that characterized parts of the Pleistocene (Dansgaard *et al.*, 1993; Jouzel *et al.*, 2007).

Given the rather polarized nature of the differences between regions that were recovered in this study, and given the more or less clear differences between conditions presented in the different epochs, this result offers an immediate means of contemplating the plausibility of certain molecular dating results, as they may indicate speciation events at times that were not characterized by range fragmentation. For example, the assertion (Zink & Slowinski, 1995; Klicka & Zink 1997) of pre-Pleistocene speciation for North American vertebrates does not appear to be supported by this viewpoint: North American species ranges are relatively continuous and not fragmented in warm periods, so Pliocene speciation (when climates were even warmer than at present) is probably not a viable explanation for their patterns of differentiation. Rather, these species'

ranges are fragmented during globally cool periods, such as during the Pleistocene, suggesting that the molecular dating of these splits may be inaccurate. Similar arguments apply to the timing of speciation in the Amazon Basin, which has been broadly asserted to pre-date the Pleistocene, at least for vertebrates (see review in Bush, 1994): Pliocene speciation in the Amazon would seem unlikely, however, as species' distributions were probably more connected and less fragmented under those conditions. Clearly, more in-depth testing is needed (indeed, Pliocene climate scenarios are under development for use in niche modelling applications), but adding an ecological perspective to the purely temporal viewpoint has much to offer.

More generally, our results offer a view of a richer, more *geographic* version of phylogeography (Peterson, 2009). The present suite of molecular tools and coalescent-based analyses offers rich insights into population history, patterns of historical demography and a general indication of the effects of the geographic template (i.e. multiple allopatric clades, a single clade with no marked differentiation, etc.). However, they cannot aid in identification of specific geographic, temporal and landscape factors associated with speciation. Niche modelling techniques to date have provided proofs of concept, applications to specific cases of interest and new means for posing hypotheses for testing with phylogeographic methods. The techniques and ideas marshalled in this paper thus offer an integrative view of the effects of the geographic template on the processes and accumulation of biological diversity. Thus, with the approach we outline here, regional geographic and climatic history can be linked to molecular phylogeographic results by means of ecological niche models. It is hoped that a more synthetic understanding may emerge (Peterson, 2009).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Summary of species and sample sizes.
Appendix S2 Preliminary tests with Maxent.

BIOSKETCHES

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