



Pleistocene fragmentation of Amazon species' ranges

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ABSTRACT

Historical patterns of connection and isolation of the impressive biological diversity of the Amazon Basin have been the subject of extensive debate, based on evidence drawn from distributional patterns of endemic species, vegetation histories from palynological studies, and geological studies. We develop species-specific ecological niche models based on current occurrence patterns of 17 species of birds and woody plants, which we project onto modelled Pleistocene (Last Glacial Maximum) climatic patterns to reconstruct past potential distributions of each species. Forest species' distributions showed fragmentation at Last Glacial Maximum and these fragments were coincident spatially, whereas savanna species showed no clear trends. Our results suggest that past climate changes fragmented forest species' ranges within a matrix of uncertain composition.

Keywords

Amazon, biogeography, ecological niche modelling, last glacial maximum, Pleistocene.

INTRODUCTION

The historical events that produced high species diversity in many taxonomic groups in the Amazon Basin remain controversial (Haffer, 1997; Colinvaux *et al.*, 2000; Gascon *et al.*, 2000; Knapp & Mallet, 2003), although most explanations have focused on geographical isolation of populations, not only has intense research attention failed to achieve any consensus, but the same data have been interpreted towards radically different conclusions (Bush, 1994; Haffer, 1997; Colinvaux *et al.*, 2000). New evidence in recent discussions consisted of additional phylogenetic and phylogeographical studies (e.g. Hall & Harvey, 2002; Aleixo, 2004) and additional palynological sampling points with vegetation histories (Colinvaux *et al.*, 1996; Hoorn, 1997; Haberle & Maslin, 1999; de Freitas *et al.*, 2001; Ledru *et al.*, 2001).

A key element in distinguishing among different hypotheses is the phenomena that *cause* the spatial disjunctions and consequent isolation of populations. Whereas the forest refuge hypothesis is based on the idea of dry-climate-driven forest fragmentation and savanna expansion as prime determinants of Amazonian biological diversification (Haffer, 1997), the riverine barrier hypothesis appeals to existing rivers as barriers (Ayres & Clutton-Brock, 1992), and the marine transgression hypothesis deals with the effects of rising sea levels during past climatic fluctuations (Frailey *et al.*, 1988; Frailey, 2002). Others have pointed out the possibility of Pleistocene climate-induced heterogeneity fragmenting species distributions within a forested matrix (Bush, 1994), an idea that has garnered some recent support (Haberle & Maslin, 1999; Cowling *et al.*, 2001; Ledru *et al.*, 2001).

Herein, we bring a distinct body of evidence — species-specific ecological niche models based on present-day occurrences, projected onto Pleistocene Last Glacial Maximum (LGM; 21,000 yr BP) climate reconstructions — to test whether the basic predictions of key hypotheses (e.g. were forest species' now-continuous ranges fragmented at LGM?) are supported. This general approach has been validated quantitatively for North American mammals (Martínez-Meyer *et al.*, 2004), and has been proven to be able to reconstruct patterns of both dramatic change and marked stasis in species historical distributions (Martínez-Meyer *et al.*, 2004; Peterson *et al.*, 2004). Given the documented conservatism of these modelled ecological niches over evolutionary time periods (Peterson *et al.*, 1999; Martínez-Meyer *et al.*, 2004), we project them onto two independent climate reconstructions for LGM (Pope *et al.*, 2002; McFarlane *et al.*, 1992). These niche projections provide climate-based hypotheses of LGM potential distributions for individual species, which can be used to explore how LGM climatic conditions affected forest and savanna species' distributions. It should be noted that although our results focus on LGM conditions, the general similarity among global climatic cycles through the Pleistocene (e.g. up to *c.* 10⁶ year BP) suggests that our past projections will be informative about patterns of isolation further back in history than LGM.

METHODS

Species distributions and environmental data sets

Because biodiversity data for many regions worldwide are still in early stages of computerization, we selected a limited suite of bird

and plant species for analysis, subject to the criterion that reasonable densities (> 20 points) of occurrence data be available for analysis. All occurrence data are based on information associated with specimen vouchers in natural history museums (see Appendix S1 in Supplementary Material). Six forest birds (*Automolus infuscatus*, *Campephilus rubricollis*, *Formicarius colma*, *Philydor pyrrhodes*, *Pipra coronata*, and *Tangara mexicana*) and three forest woody plants (*Rauvolfia paraensis*, *Rauvolfia polyphylla*, and *Rauvolfia sprucei*) — a total of 398 occurrence points, and five savanna birds (*Athene cunicularia*, *Sublegatus modestus*, *Ammodramus humeralis*, *Emberizoides herbicola*, and *Sporophila plumbea*) and three savanna woody plants (*Rauvolfia weddelliana*, *Rauvolfia ligustrina*, and *Curatella americana*) — a total of 334 occurrence points, were obtained from ornithological and botanical collections (see Acknowledgements) and georeferenced to the nearest 1' of latitude and longitude.

Niche models were based on present climatic data (1961–90; annual mean precipitation and temperature) provided by the Intergovernmental Panel on Climate Change,¹ and topographical information (elevation, slope, aspect, compound topographical index) from the US Geological Survey's Hydro-1K² data set. All coverages were resampled at 0.1° pixel resolution and clipped to northern South America (9°–18°30' S, 80°–44° W) for model development. Once current ecological niche models were developed, we projected them onto two LGM climate scenarios, drawn from the Hadley and Canadian climate modelling centres' results in the Palaeoclimate Modelling Intercomparison Project (PMIP, 2000) data archives.³ All analyses were restricted to the Amazon Basin (forest species), or a slightly broader swath of northern South America (savanna species).

Ecological niche modelling

Niche models were developed using the Genetic Algorithm for Rule-set Prediction (GARP⁴; Stockwell & Noble, 1992; Stockwell & Peters, 1999). This procedure focuses on modelling ecological niches: the conjunction of ecological conditions within a species is able to maintain populations without immigration (Grinnell, 1917). GARP relates ecological characteristics of known occurrence points to those of points randomly sampled from the rest of the study region, developing series of decision rules that best summarize those factors associated with the species presence (Peterson *et al.*, 2002). Extensive testing has demonstrated GARP's ability to predict ecological and geographical distributions of species in diverse ecological, geographical, temporal, and taxonomic contexts (Peterson & Cohoon, 1999; Peterson, 2001; Stockwell & Peterson, 2002a,b, 2003; Anderson *et al.*, 2003; Martínez-Meyer *et al.*, 2004).

Occurrence points are first divided into training and test data sets. Then, GARP applies an iterative process of rule selection,

evaluation, testing, and incorporation or rejection. It chooses a method from a set of possibilities (e.g. logistic regression, bioclimatic rules) applied to the training data, and a rule is developed or evolved; rules may evolve by a number of means (e.g. truncation, point changes, crossing-over) to maximize predictivity. Predictive accuracy (for intrinsic use in the model refinement) is then evaluated based on 1250 points sampled randomly from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1000 iterations or until convergence. Because GARP uses a random-walk approach and predictions vary between runs, we generated 100 models per species, and selected the 10 'best' models (those falling in an optimal combination of error measures) following recent recommendations (Anderson *et al.*, 2003). These 10 models were summed to obtain maps for both present and past (Hadley and Canadian) potential distributions for each species.

Fragment analysis

To study the effects of LGM climates on extent and configuration of species distributions, we measured features related to fragmentation in FRAGSTATS version 3.3 (McGarigal *et al.*, 2002), as follows. Potential distributions of each species were reclassified to binary predictions: those areas with high model agreement in prediction of presence (> 5 of 10 models) were considered predicted present. To permit area comparisons, maps were reprojected to a Lambert Azimuthal Equal-Area projection in ARCFINFO 8.3 (ESRI, 2002), and imported into FRAGSTATS as ArcGrid (raster) files.

A standard FRAGSTATS analysis was performed on the whole landscape (Landscape option). Beyond simple distributional areas, two fragmentation metrics were captured: landscape shape index (LSI; LSI = 1 when the landscape consists of a single square, or almost square, patch, and increases without limit as landscape shape becomes more irregular and/or as the length of edge within the landscape increase); and landscape division index (LDI; LDI = 0 when the landscape consists of single patch, achieving its maximum value when the landscape is maximally subdivided). Detailed descriptions of all metrics are available in the FRAGSTATS documentation (McGarigal *et al.*, 2002). Mann–Whitney *U*-tests were used to test for differences in fragmentation metrics between present distributions and LGM projections.

Coincidence of LGM distributions

To ask whether LGM fragments of forest species' ranges were spatially coincident across species, we averaged the two climatic scenarios and reclassified them to a binary prediction, based on a threshold that yielded a prediction of *c.* 10% of total area of the Amazon Basin predicted present. The result of these initial transformations was a set of LGM distributional predictions (one per species) that included approximately the same proportion of the Amazon Basin as habitable for each species.

¹<http://www.ipcc.ch/>

²<http://edcdaac.usgs.gov/gtopo30/hydro/>

³<http://www-lsce.cea.fr/pmip/>

⁴<http://www.lifemapper.org/desktopgarp/>

Table 1 Changes in predicted distributional area, landscape shape index (LSI), and landscape division index (LDI) for modelled potential distributions of forest and savanna species at present-day and Last Glacial Maximum (Canadian and Hadley scenarios)

| | Present | | | Hadley | | | Canadian | | |
|--------------------------------|----------------------|-------|------|----------------------|-------|------|----------------------|-------|------|
| | Area km ² | LSI | LDI | Area km ² | LSI | LDI | Area km ² | LSI | LDI |
| Forest species | | | | | | | | | |
| <i>Automolus infuscatus</i> | 6,161,543 | 3.88 | 0.00 | 4,999,980 | 9.30 | 0.04 | 2,856,186 | 8.67 | 0.20 |
| <i>Campephilus rubricollis</i> | 6,672,568 | 5.10 | 0.00 | 4,999,980 | 6.86 | 0.02 | 2,856,186 | 6.80 | 0.21 |
| <i>Formicarius colma</i> | 6,308,931 | 8.67 | 0.00 | 3,642,658 | 9.30 | 0.04 | 3,268,268 | 12.14 | 0.20 |
| <i>Philydor pyrrohodes</i> | 6,584,860 | 7.35 | 0.01 | 5,425,569 | 34.95 | 0.63 | 3,022,662 | 10.98 | 0.23 |
| <i>Pipra coronata</i> | 6,420,801 | 20.04 | 0.02 | 5,273,228 | 27.09 | 0.10 | 2,761,592 | 22.62 | 0.29 |
| <i>Tangara mexicana</i> | 5,741,608 | 9.68 | 0.01 | 4,502,824 | 15.31 | 0.03 | 2,670,139 | 31.23 | 0.27 |
| <i>Rauvolfia paraensis</i> | 5,465,920 | 5.55 | 0.01 | 1,056,603 | 37.19 | 0.72 | 2,980,982 | 10.63 | 0.14 |
| <i>R. polyphylla</i> | 3,229,005 | 6.92 | 0.25 | 1,282,517 | 20.13 | 0.78 | 1,099,611 | 8.24 | 0.35 |
| <i>R. sprucei</i> | 6,917,691 | 15.66 | 0.00 | 6,811,016 | 17.79 | 0.01 | 5,369,997 | 16.70 | 0.01 |
| Savanna species | | | | | | | | | |
| <i>Athene cunicularia</i> | 1,393,179 | 31.81 | 0.49 | 1,120,269 | 52.75 | 0.90 | 1,990,342 | 49.66 | 0.43 |
| <i>Sublegatus modestus</i> | 1,583,213 | 43.06 | 0.79 | 3,104,812 | 42.67 | 0.41 | 3,101,430 | 35.64 | 0.11 |
| <i>Ammodramus humeralis</i> | 2,750,115 | 65.46 | 0.28 | 3,099,134 | 46.38 | 0.45 | 2,201,880 | 60.56 | 0.74 |
| <i>Emberizoides herbicola</i> | 2,525,771 | 57.22 | 0.80 | 1,150,472 | 36.47 | 0.82 | 3,099,134 | 46.38 | 0.45 |
| <i>Sporophila plumbea</i> | 1,113,142 | 59.23 | 0.98 | 433,949 | 50.6 | 0.99 | 1,099,853 | 55.2 | 0.96 |
| <i>Rauvolfia weddelliana</i> | 926,491 | 27.63 | 0.78 | 1,150,472 | 36.47 | 0.82 | 1,576,931 | 38.75 | 0.77 |
| <i>R. ligustrina</i> | 504,071 | 15.00 | 0.45 | 48,684 | 10.56 | 0.79 | 346,571 | 21.6 | 0.86 |
| <i>Curatella americana</i> | 3,028,461 | 53.29 | 0.20 | 2,744,558 | 62.47 | 0.59 | 2,425,861 | 50.29 | 0.50 |

Non-randomness of coincidence among fragments was assessed in two ways. (1) Grid squares were treated independently, and expected overlap probabilities between each species pair were calculated as the products of proportional area predicted present for each species. (2) Range polygons of area > 12,000 km² were treated as units, conserving patterns of spatial autocorrelation; here, for each species, 10 range polygons were moved randomly within the Amazon Basin (no overlap permitted between polygons). Observed overlap between species was then compared with that in the randomized distributions. Statistical significance of these comparisons was established based on sign test comparisons of observed and expected overlaps across all pairwise combinations of species, setting N to the number of species, rather than to the number of pairwise comparisons.

RESULTS

All nine forest species showed reductions in potential distributional area (LGM range 19–98%, median 53%, of present distributional area), as well as increases in edge complexity (LSI) and landscape subdivision (LDI) at LGM under both scenarios (Table 1). Analysed as a whole, LGM climates had significant effects on all three measures (Mann–Whitney U -tests; area reduced at LGM, LSI, and LDI increased at LGM, all $P < 0.05$). Although the two scenarios were developed from independent palaeoclimatic models (McFarlane, 1992; Pope *et al.*, 2002), we found no significant differences between their predictions of LGM distributions. Hence, forest species' LGM ranges were reconstructed as being reduced in area and more fragmented.

LGM distributions of forest species were generally reconstructed as having split into eastern and western segments, and in some cases, into smaller fragments within those areas (Fig. 1). It is particularly intriguing that the areas into which forest species likely fragmented were not independent of one another — rather, they were highly spatially coincident across species (Fig. 2), a result established via two tests. (1) Assuming that probability of occurrence of species in each grid square is independent of that in each other grid square, observed coincidence among LGM ranges of pairs of species (i.e. based on their proportional coverage of the basin) always exceeded that expected by chance (sign test, $P < 0.05$). (2) If, on the other hand, autocorrelation patterns are maintained (see Methods), observed levels of coincidence exceeded in every case those in randomizations that maintained observed distributions of range fragment size (sign test, $P < 0.05$). Hence, species-specific LGM range fragments were spatially coincident, across species suggesting that forest species assorted into consistent areas at LGM.

Only two (*S. modestus* and *R. weddelliana*) of eight savanna species analysed (Table 1) were reconstructed as having an unambiguously broader and more continuous potential distribution at LGM. Other savanna species analysed, however, had expanded LGM potential distributions for the Hadley scenario, but reduced LGM distributions for the Canadian scenario, or vice versa; hence, no clear directionality of change was observed among savanna species in either range size or fragmentation indices (Mann–Whitney U -tests, all $P > 0.05$). Two representative examples of modelled LGM potential distributions of savanna species are shown in Fig. 3.

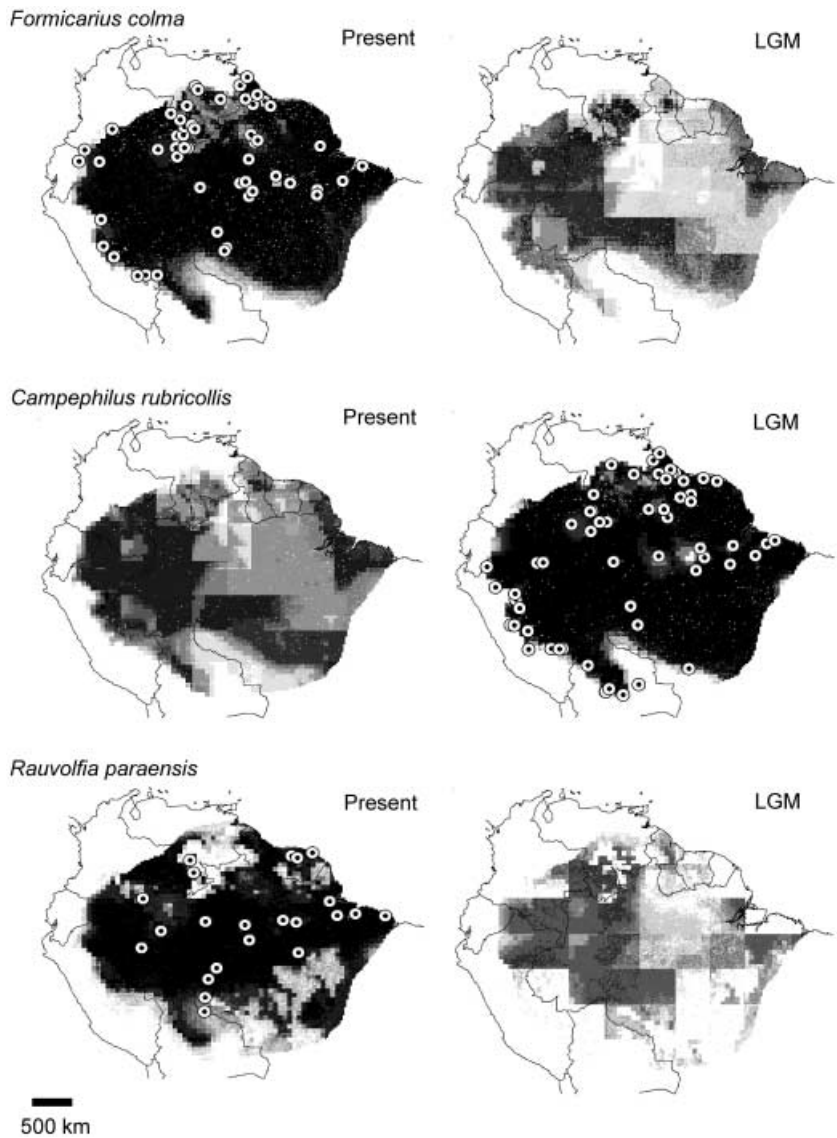


Figure 1 Present-day and Last Glacial Maximum (Hadley and Canadian scenarios averaged) potential distributions for *Formicarius colma*, *Campephilus rubricollis*, and *Rauvolfia paraensis* in the Amazon Basin. Dots on present-day maps show occurrence data on which ecological niche models were based. Darker shading indicates greater model agreement in predicting potential presence.

DISCUSSION

Our methods and results are independent of and complementary to previous evidence marshalled to the debate about Amazon biogeography in the late Pleistocene, being based solely on present-day ecological characteristics of occurrences of species in the region. In contrast to earlier work based on *known* occurrences of forest species (Brown, 1987; Prance, 1987), use of ecological modelling for estimating potential distributions avoids problems of incomplete sampling across the region (see Nelson *et al.*, 1990).

Fragmentation of forest species' potential LGM distributions is consistent with climate-driven changes in species distributions during the Pleistocene. Additionally, two interesting patterns emerge from our results: (1) they do not support an important prediction of the original refuge hypothesis — broad expansion of savanna species' distributions into currently forested areas, and (2) LGM distributions of forest species

are highly coincident and split into eastern and western segments, and in some cases, into smaller fragments within those areas, especially in the northern and eastern portions of the Amazon.

Haffer's (1969) hypothesis of forest refugia emerged from coincident vertebrate distributions assorted in specific pockets on the periphery of the Amazon Basin, and evidence that supported the idea of ice-age aridity in South America (e.g. Garner, 1959, 1966; more recently van der Hammen, 1974; van der Hammen & Absy, 1994). The argument for extreme aridity in the Amazon during the Pleistocene has been weakened by reanalysis of previous information (Colinvaux *et al.*, 2000; Pennington *et al.*, 2000) and addition of new palaeoecological data (pollen analysis of the Amazon Fan, Hoorn, 1997 and Haberle & Maslin, 1999; but see Pennington *et al.*, 2000 for a critique on reliability of Amazon fan deposits; palinological data across the basin, Colinvaux *et al.*, 2000; carbon isotopes of soil organic matter, de Freitas *et al.*, 2001).

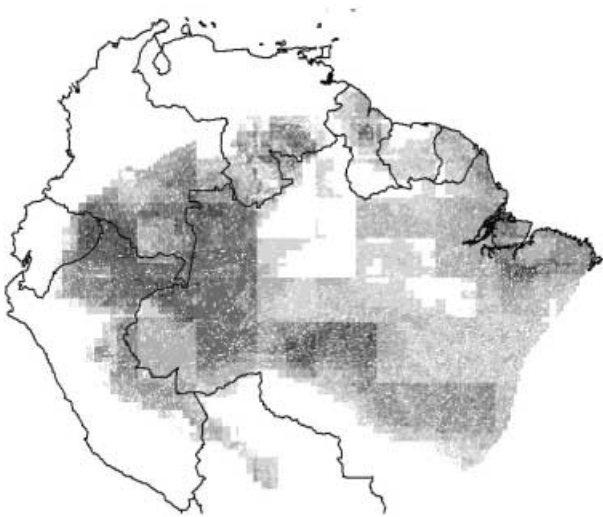


Figure 2 Last Glacial Maximum potential distributions of forest species, showing patterns of coincidence among range fragments reconstructed for forest species. Potential distributions of each species were reclassified to binary predictions based on a threshold of *c.* 10% of total area (the Amazon Basin) predicted present; these binary grids were summed to produce this surface showing potential species richness of forest species (darker shades indicating more species overlapping).

However, it has been suggested that moderate decreases in rainfall (10–20%, Bush, 1994; Simpson, 1997) or carbon limitation and water stress due to lowered atmospheric CO₂ concentrations during LGM (Cowling *et al.*, 2001; Mayle *et al.*, 2004) may

have affected peripheral areas of the Amazon Basin, producing minor vegetation shifts (Behling & Hooghiemstra, 1999; Mayle *et al.*, 2000; da Silveira & Sternberg, 2001). Plausible scenarios for less stable forest cover and composition in the margins of the Amazon are consistent with peripheral fragmentation observed in our LGM reconstructions (Figs 1 & 2).

More interestingly, our full suite of rainforest taxa was not reconstructed as finding habitable conditions in the intervening areas between the major western and eastern LGM forest blocks. If savanna species did not invade, then, what kind of vegetation was occupying those areas at LGM? Recent biogeographical research raises the possibility that much of the Amazon Basin was instead occupied by seasonally dry tropical forest during the last glacial period (i.e. Dry Forest Arc hypothesis; Prado & Gibbs, 1993; Pennington *et al.*, 2000, 2004). Pennington *et al.* (2000) argued that glacial pollen spectra from Amazonia, previously interpreted as a continuous rainforest signal with intrusion of some Andean elements (Colinvaux *et al.*, 1996; Colinvaux *et al.*, 2000), could be interpreted as a predominantly seasonally dry forest signal. Most dry forest families are a subset of rainforest families, and, since most pollen cannot be identified to species, it is virtually impossible to distinguish these ecosystems (Pennington *et al.*, 2000). To test the Dry Forest Arc hypothesis, Mayle *et al.* (2004) used dynamic vegetation model simulations for LGM, and recovered considerable reduction (and some fragmentation) of rainforest on the southern fringe, and expansion of the southern dry forests towards the northward. Nonetheless, expansion of the northern dry forests southward and retraction of the northern fringe of the rainforest were not observed. Modelling potential distributions of dry forest species and testing their

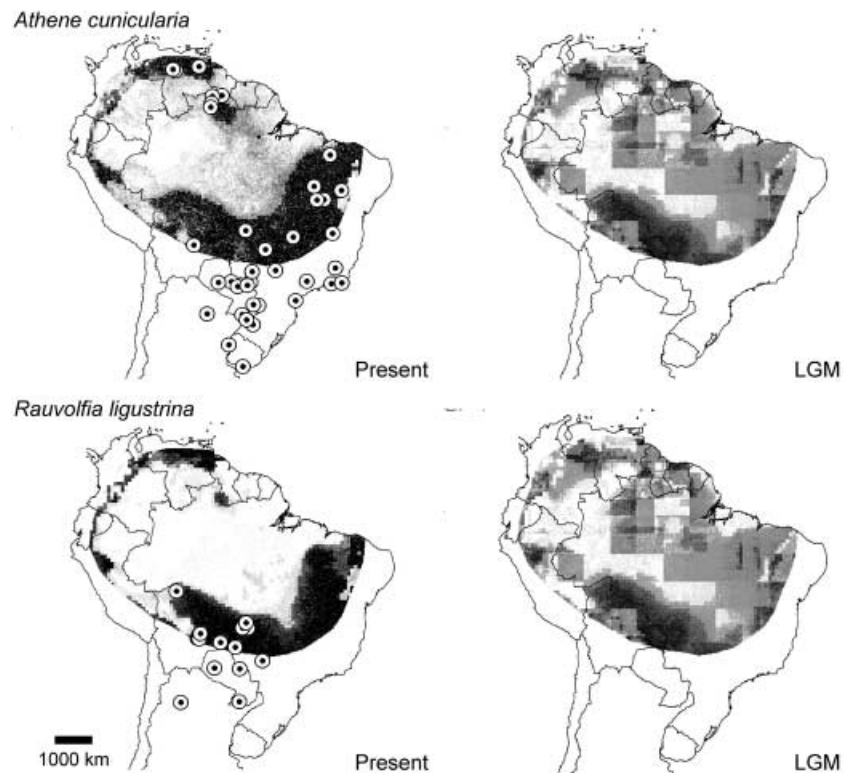


Figure 3 Present-day and Last Glacial Maximum (Hadley and Canadian scenarios averaged) potential distributions for *Athene cucicularia* and *Rauvolfia ligustrina*. Dots on present-day maps show occurrence data on which ecological niche models were based. Predictions are restricted to savannas surrounding the Amazon Basin. Darker shading indicates greater model agreement in predicting potential presence.

possible LGM range shifts can contribute to assessing whether ecological conditions in areas separating the rainforest fragments were suitable for establishment of dry forest ecosystems.

Whether observed LGM fragmentation is associated with phenomena responsible for the biological diversification in the Amazon is a subject still in need of attention. Pleistocene speciation of Amazon forest species has been rejected in multiple studies based on molecular clocks and population genetic studies (reviewed in Moritz *et al.*, 2000; but see Richardson *et al.*, 2001). Nonetheless, assumptions regarding accuracy of molecular clocks and constancy of rates of evolution are fraught with uncertainty (Peterson, 1992; Zhang & Ryder, 1995; Graur & Martin, 2004); population studies based on single genes or non-neutral markers also have their caveats (Rand, 1996). Biological evidence supporting other hypotheses (e.g. riverine barriers) is equivocal (Gascon *et al.*, 2000; Moritz *et al.*, 2000) and, as such, the debate about Amazon diversification is far from resolved. Perhaps the best interpretation of our results is that the complexity of Amazon Basin habitats increased for the species we examined, producing greater heterogeneity in the region; some of these conditions were likely inimical to forest species in some areas, leading to coincident, fragmented ranges of forest species at LGM.

Although the conservative nature of niche evolution has been tested and supported (Huntley *et al.*, 1989; Peterson *et al.*, 1999; Peterson, 2003), many features of our models could be improved — finer-scale (in space and time) palaeoclimate reconstructions need to be explored and their assumptions considered and tested profoundly. Clearly, the number of species and density of present-day occurrence data could also be improved. Nonetheless, this first suite of LGM reconstructions strongly supports the idea of climate-driven fragmentation of potential distributions of individual species in Amazon forests.

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SUPPLEMENTARY MATERIAL

The following material is available as part of the full-text article on www.blackwell-synergy.com/loi/ddi.

Appendix S1 Geographical coordinates for forest and savanna species of birds and plants analysed in this study.