

## Trans-Amazon dispersal potential for *Crotalus durissus* during Pleistocene climate events

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**Abstract:** Two disjunct distributional areas of *Crotalus durissus* (Neotropical rattlesnake) are in open habitats north and south of the Amazon Basin and are presently separated by humid rainforest habitats. We used ecological niche modeling to identify and investigate potential dispersal pathways for this species between the two areas during the late Pleistocene. Niches estimated for the two populations did not differ significantly. Our analyses indicated two possible, but a single most likely, potential routes of dispersal during the last glacial cycle. These results are important to understanding the history of Amazon Basin humid forest biotas, as they suggest agents of isolation among putative humid forest refugia in the form of dry forest and scrub, and associated biotas.

**Keywords:** Ecological Niche Modeling, Amazon Basin, Biogeography, Forest Refugia, Last Glacial Maximum.

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**Resumen:** Actualmente existen dos áreas de distribución disjuntas de la serpiente de cascabel *Crotalus durissus*, afín a hábitats abiertos, al norte y al sur de la cuenca del Río Amazonas, separadas por selvas húmedas. Usamos técnicas de modelado de nicho ecológico para identificar corredores potenciales de dispersión para esta especie entre las dos áreas en el Pleistoceno tardío. Los nichos estimados para las poblaciones de cada una de las áreas de distribución no presentaron diferencias significativas. Nuestros análisis identificaron un corredor de dispersión más probable para esta especie durante el Último Máximo Glaciar. Estos resultados tienen implicaciones para el entendimiento de la historia de las biotas de las selvas húmedas del Amazonas, ya que sugieren causas de aislamiento entre refugios potenciales de selva húmeda, en la forma de selva seca y matorral.

**Palabras-chave:** Modelado de Nicho Ecológico, Amazonas, Biogeografía, Refugios Pleistocénicos, Último Máximo Glaciar.

### Introduction

The events leading to the present diversity of species across the Amazon Basin have been pondered since the time of Darwin (Mayr and O'Hara 1986, Nores 1999, Bush and de Oliveira 2006). However, effects of past climate shifts on present-day biotic diversity can be difficult to discern because they depend on complex interactions among multiple biotic and abiotic factors. Earliest assumptions were of stable tropical rainforest ecosystems that had remained largely unchanged since the Cenozoic (Fischer 1960, Bush 1994, Nores 1999). This idea was replaced by the Pleistocene Refugium Hypothesis (PRH) beginning in the late 1960s (Haffer 1969), and gaining considerable popularity thereafter. Given improved understanding of geologic history and impacts on climate and hydrologic systems, the PRH provided a more adequate explanation of the distribution and diversity of modern taxa in the region.

The PRH posits substantial retractions and fragmentation of humid rainforests in the face of advancing savannahs during the cooler, drier climates of the Last Glacial Maximum (LGM, ~21,000–18,000 yr BP) and preceding glacial events.

This hypothesis has been resurrected and amended in various forms (Mayr and O'Hara 1986). However, as data from sedimentary core samples from across the Amazon Basin and marine isotope analyses shed light on climatic cycles and likely regional vegetation responses throughout the Quaternary (van der Hammen and Hooghiemstra 2000, Bush 1994, Bush and de Oliveira 2006), researchers have suggested more moderate explanations for Pleistocene range fragmentation, such as increased vegetation heterogeneity in the region, perhaps with dry-forest conditions constituting the cool-climate matrix rather than savannah (Nores 1999, Bonaccorso et al. 2006, Peterson and Nyári 2008, Bush et al. 2011).

The Pleistocene (~2.58 My-11.7 Ky BP) saw a series of global cooling events alternating with warmer periods: temperature fluctuations averaged 4–5°C, and precipitation varied by 50–60% (van der Hammen and Hooghiemstra 2000, Bush and de Oliveira 2006, Lawing and Polly 2011). Paleoreconstructions of the Last Interglacial period (LIG; ~130,000–116,000 yr BP) indicate climates similar to or possibly even warmer than those of the present day (Otto-Bliesner et al. 2008), whereas the LGM (~21,000–18,000 yr BP)

was characterized by cold and dry climates in continental regions worldwide (van der Hammen and Hooghiemstra 2000, Braconnot et al. 2007). Ehlers and Gibbard (2007) suggested at least 20 glacial cycles over the previous 2.6 My BP, most within the last ~900,000 yr.

Ecological niche modeling (ENM), in combination with paleoclimatic reconstructions, provides researchers with a powerful tool with which to “retrodict” potential past distributions of species for key points in time (e.g., LIG, LGM), and can be particularly useful for investigating hypotheses such as the PRH (Waltari et al. 2007, Peterson and Nyári 2008). Availability of climatic reconstructions for the Pleistocene allows exploration of paleo-distributional potential of species, including the location and timing of range disjunctions and potential dispersal routes. Although previous ENM studies of Amazon Basin biotas have indicated that distributions of forest species did fragment owing to climate changes (Bonaccorso et al. 2006, Peterson and Nyári 2008), few have reconstructed the converse phenomenon of broadened distributions of savannah species (Bonaccorso et al. 2006, Collevatti et al. 2012).

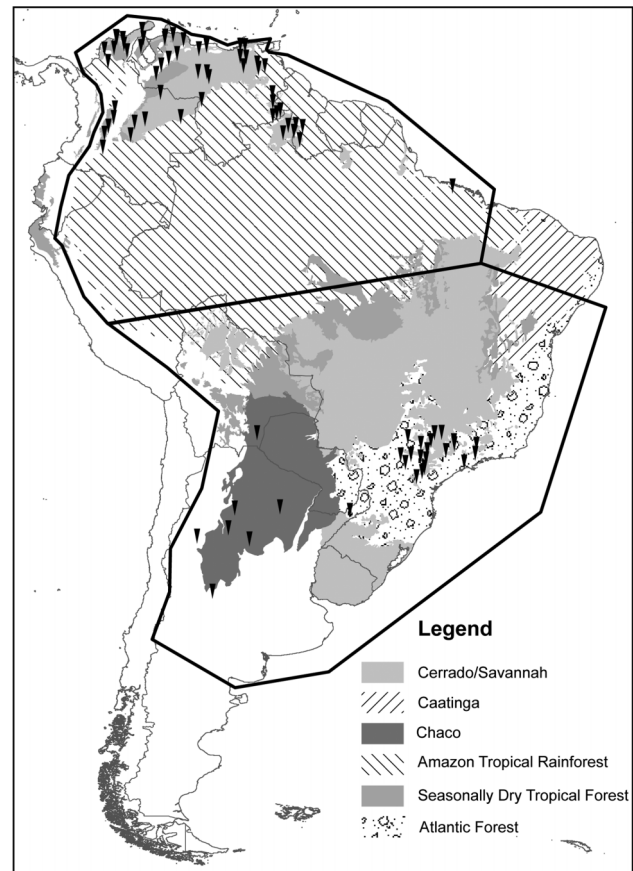
Here, we use LGM and LIG paleoclimatic reconstructions in an ENM framework to understand possible effects of Pleistocene climatic shifts on Amazon Basin habitats via analysis of an open-habitat species, the rattlesnake *Crotalus durissus* L., 1758. Despite high diversity of rattlesnakes in North America, *C. durissus* is the only rattlesnake species to have colonized South America broadly (Tozetti and Martins 2008). Populations of this species are found across a broad range in Mesoamerica, and in South America north and south of the Amazon Basin. Though predominantly found in the *cerrado* formations known as *campo cerrado* and *campo sujo*, (Wüster et al. 2005a, Quijada-Mascareñas et al. 2007), *C. durissus* populations are also known from fragmented dry forest habitats and disturbed areas (Bastos et al. 2005, Quijada-Mascareñas et al. 2007, Tozetti and Martins 2008, Tozetti et al. 2009). As a result, a distributional understanding for this species through time may be particularly illuminating as regards the distributional history of Amazonian biotas.

## Materials and Methods

### 1. Input Data

Occurrence data for six disjunct populations of the *C. durissus* complex across Central and South America were kindly provided by A. Quijada-Mascareñas (pers. comm.). In light of the coarse spatial resolution of available paleoclimatic reconstructions, we focused analyses on the two populations in South America, for which 55 unique occurrences for the northern population and 28 occurrences for the southern population (Figure 1) were available. As these sets of occurrences are distinctly located north and south of the Amazon Basin, their potential for range shifts during Pleistocene cooling events is of particular relevance.

Present-day climatic data were acquired from the WorldClim database (Hijmans et al. 2005). Parallel Late Pleistocene bioclimatic layers (LGM and LIG) were derived from downscaled global climate outputs from the Community Climate System Model (CCSM). LGM data were obtained from the Paleoclimate Modeling Intercomparison Project Phase II (PMIP2, Braconnot et al. 2007); LIG data (~140,000–120,000 yr BP) were kindly



**Figure 1.** Model calibration regions for *Crotalus durissus* overlaid on a map of ecoregions (Olson et al. 2001). Thick black line delineates training regions (M) for northern and southern populations; triangles indicate present-day *C. durissus* occurrence points used in this study.

made available by C. Ammann (pers. comm.), based on Otto-Bliesner et al. (2006), and downscaled and prepared by R. Hijmans (pers. comm.). As a result, we were able to characterize distributional responses to major climatic events over the past 135,000 yr. Because robustness of ENMs is highly dependent on the complexity of the environmental spaces in which they are calibrated (Peterson and Nakazawa 2008, Peterson et al. 2011), we took care not to calibrate models in highly dimensional spaces. Seven variables showing low correlations (<0.8) were used in ENM calibration (annual mean temperature, mean diurnal range, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, and precipitation of wettest and driest months). All analyses were conducted at a spatial resolution of 2.5', or ~5 km.

Model calibration regions were delineated carefully, as most presence-only niche modeling algorithms generate background information, or pseudoabsences, based on these areas (Stockwell 1999, Phillips et al. 2006, Pearson et al. 2007, Warren et al. 2010). In this step we followed Barve et al. (2011): we attempted to identify areas that had been accessible to the species over relevant time periods, whether suitable or not, in effect a hypothesis of M in the Biotic-Abiotic-Mobility (BAM) framework (Peterson et al. 2011). These hypothesized accessible areas were bounded to the west by the eastern foothills of the Andes and to the east by the Atlantic Ocean.

The calibration area for the northern population extended north to encompass the full extent of the coastline; that of the southern population extended south into north-central Argentina. Designation of the accessible area in the Amazon Basin was chosen arbitrarily at roughly half the distance between the known occurrence points of the two populations (Figure 1). We transferred model results to the whole of South America to allow interpretation of potential dispersal routes at a continental scale during LGM.

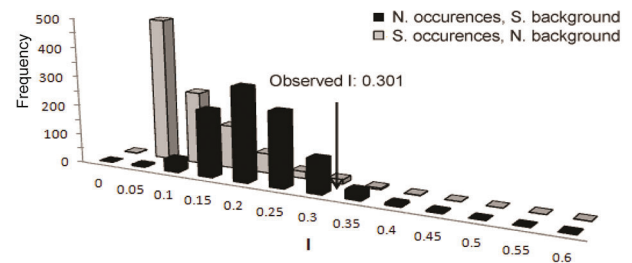
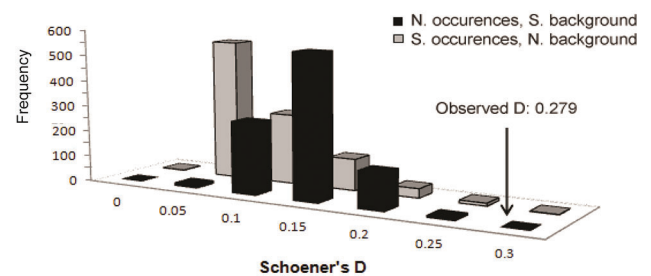
## 2. Niche Similarity

As an initial step, we used ENMTools (Version 1.3, <http://enmtools.blogspot.com/>) to test hypotheses of niche similarity between the two populations. Described in depth by Warren et al. (2010), the program works in conjunction with Maxent (Phillips et al. 2006) to test whether two populations have environmental characteristics of occurrences more or less similar than random expectations. The “background” area specified in this test for each population is the accessible area (M) described above. The program compares niche models via two similarity metrics (Schoener’s  $D$  and  $I$ ) based on known occurrences of one of the two populations with niche models based on points drawn at random from the “background” (M) of the other. This process was repeated 1000 times to create a null distribution of background similarity values. ENMs were generated for each population in Maxent, and thresholded to the least training presence value (Pearson et al. 2007). Finally, we compared observed similarity values to the null distribution, rejecting the null hypothesis of similarity if the observed fell below the fifth percentile of the distribution of null values.

## 3. Ecological Niche Modeling

Because observed values for niche similarity for both similarity metrics were well above the critical values of the null distributions (Figure 2), we were unable to reject the null hypothesis (all  $P \geq 0.997$ ); we thus accepted that no significant dissimilarity exists between niches of northern and southern South American populations of *C. durissus*. In view of these results, occurrences of the two populations were combined (i.e., the two calibration regions and occurrence data) to obtain an overview of likely geographic limits of the distribution of *C. durissus* through time.

Niches were estimated and paleodistributional projections made using two common ENM algorithms: the openModeller (OM-GARP version 1.1, Muñoz et al. 2011) implementation of the Genetic Algorithm for Rule-set Prediction (GARP, Stockwell 1999) and a maximum entropy approach (Maxent, Phillips et al. 2006). Both algorithms were set to 1000 bootstrapped runs for up to 1000 iterations of estimation. GARP models were run to a 1% convergence criterion, with extrinsic testing of omission, a relative omission threshold (20% of the distribution), and a 50% commission threshold (Anderson et al. 2003), producing 100 final models for interpretation, which were summed to produce a single map of model agreement. Maxent was set for 100 bootstrap replicates; all other settings were left at default. Suitability thresholds for interpretation of models from both algorithms were based on least training presence criteria (Pearson et al. 2006), modified to consider possible error rates ( $E$ ) of 0, 1, 5, and 10% (Peterson and Nyári 2008, Peterson et al. 2011).



**Figure 2.** Niche background similarity distributions for one-tailed testing of similarity of niches between northern and southern *Crotalus durissus* populations for  $D$  and  $I$  similarity indices. The observed degree of similarity between the two species is shown as a black arrow.

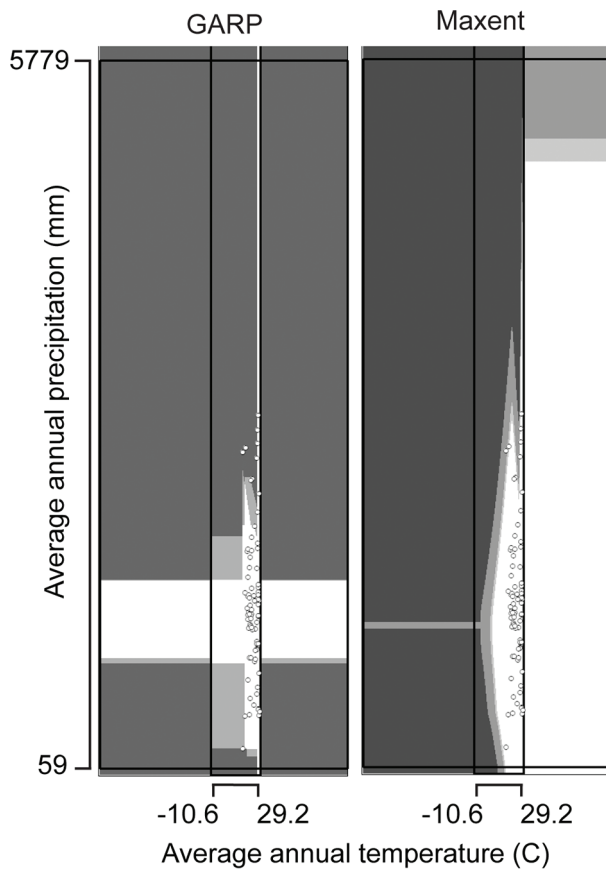
Finally, to explore responses to key climatic parameters, we developed niche visualizations following a modification of the approaches of Elith et al. (2005) and Owens et al. (2013): simple models were constructed based on two generalized bioclimatic variables (mean annual temperature and precipitation) and projected onto a two-dimensional space wherein the  $x$ -axis equates to a broad spectrum of mean annual temperatures ( $-100$ – $100^{\circ}\text{C}$ ) and the  $y$ -axis corresponds to a similar spectrum of mean annual precipitation values ( $0$ – $15,000$  mm; see Owens et al. 2013 for further illustration of this approach). ENMs were calibrated using the pooled *C. durissus* occurrence data and present-day bioclimatic data using GARP and Maxent, as described above.

## Results

The niche visualizations (Figure 3) offer a two-dimensional view of temperature and precipitation responses of the species, but also suggest the need for some caution with transferring models onto conditions outside those over which our model was calibrated (Owens et al. 2013). The two models (GARP and Maxent) differed in the response surface shape reconstructed, although which is more “correct” is not clear.

Model projections onto current conditions emphasized the disjunct nature of the present potential distribution of the species (Figure 4). Paleoprojection outputs indicated a climatically suitable dispersal corridor for *C. durissus* across the eastern part of the Amazon Basin during the cooler, drier climates of the LGM (Figure 4). GARP further identified a possible corridor from the northwest south along the eastern foothills of the Andes. Both of these corridors were in areas where projections onto LIG and present-day conditions indicated climatic barriers to trans-Amazonian dispersal (Figure 4). Visually, model outputs for the two algorithms



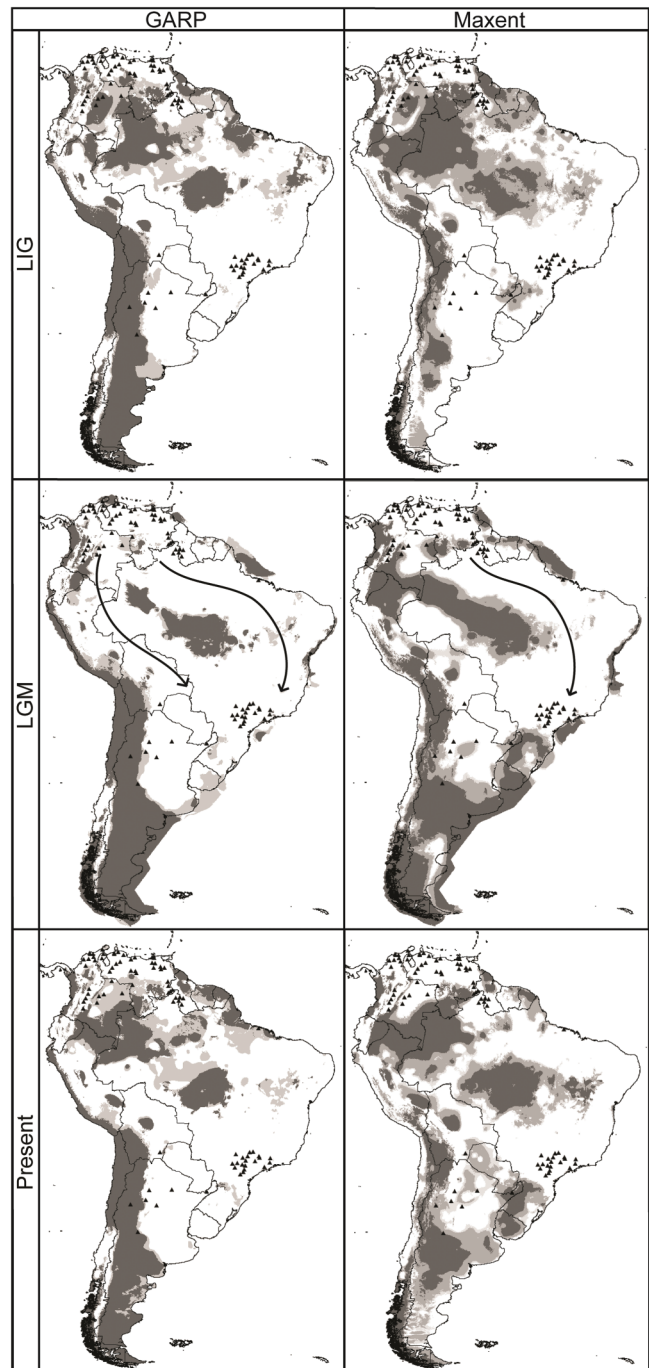


**Figure 3.** GARP (left) and Maxent (right) projections of *Crotalus durissus* occurrences and ecological niche models visualized using a calibration strip. The *x*-axis expresses mean annual temperature (-100 to 100C) and the *y*-axis shows annual precipitation (0 to 15,000 mm). Circles indicate *C. durissus* occurrences. Boxes indicate ranges of conditions manifested across the combined (north and south) calibration region.

showed high agreement as regards general patterns of bioclimatic suitability shifts across time periods. However, whereas Maxent projections showed broader areas of suitability during the transition from the LIG (22.4%) to the LGM (30.5%), GARP projected decreased suitable area from LIG (30.2%) to LGM (24.9%).

## Discussion

Our paleodistributional reconstructions concur with those of prior ENM-based studies indicating LGM expansion of *cerrado* and other dry-habitat biomes (Collevatti et al. 2012, Bonatelli et al. 2014), as well as those which identified LGM barriers for forest that coincide with our reconstructed dispersal corridors for a non-forest species (Bonaccorso et al. 2006, Peterson and Nyári 2008). Although projections from niche modeling algorithms presently provide only a single, generalized snapshot of climatic suitability for a given time slice, they illuminate processes affecting the broader distributional potential of *C. durissus* since the LIG. A variety of studies, including genetic (Wüster et al. 2005a,b, Quijada-Mascareñas et al. 2007), paleoecological (Prado and Gibbs 1993, Pennington et al. 2000, Mayle et al. 2004, Pennington et al. 2004, Anhuf et al. 2006, Cowling 2011, Hannah et al. 2011), and paleoclimatic (Colinvaux and de Oliveira 2001,



**Figure 4.** Projections of modeled potential distributional areas for *Crotalus durissus* during the Last Interglacial, Last Glacial Maximum (LGM), and the present day. Black lines indicate climatically suitable dispersal corridors reconstructed at LGM. Suitability is indicated by shading, with white denoting areas of high climatic suitability, light gray moderate suitability, and dark gray low suitability. Black triangles indicate present-day occurrence points.

Wang et al. 2004, 2006, Kanner et al. 2012, Mosblech et al. 2012) analyses, further support for these ideas. These results suggest a stepping-stone-like series of dispersal events across a heterogeneous topography dictated by effects of glacial-interglacial cycles (Vegas-Villarrúbia et al. 2012) and strongly influenced by the North Atlantic climate (Fritz et al. 2010).

Though still not completely clear, overall understanding of late Pleistocene climatic events and biotic responses in the Amazon Basin has improved significantly in recent years. The vast majority of data feeding this understanding of South America's climate during the Pleistocene derive from sites along the Atlantic seaboard and in the central Andes (Wang et al. 2004, Whitney et al. 2011); however, limited data also now exist for South America's continental interior (Whitney et al. 2011). While paleoclimatic reconstructions from the coastal and Central Andean regions suggest an overall increase in summer monsoon activity during the LGM, Whitney et al. (2011) concluded that South America's continental interior and lowlands regions experienced significantly drier conditions. Generally, the Last Glacial period (10-110 Ky BP) was characterized by abrupt, millennial-scale climatic fluctuations correlating with northern glacial-interglacial cycles (Wang et al. 2004, 2006, Kanner et al. 2012, Mosblech et al. 2012). Varying in duration from a few hundred years to several thousand, episodes of high precipitation during active summer monsoons appear to have been associated with northern stadials (LGM, 20-25 Ky BP; Heinrich event 1, 15-17 Ky BP; and Younger Dryas, 11-13 Ky BP), while drier periods were associated with reduced monsoonal activity and interglacial events in the Northern Hemisphere (Wang et al. 2004, 2006, Zech et al. 2008, Kanner et al. 2012).

The frequency and variable durations of these events may have presented opportunities for periodic dispersal events by *C. durissus* southward across the Amazon Basin as variable climatic conditions expanded and contracted suitable habitat patches (Vegas-Vilarrúbia et al. 2012). Indeed, paleovegetation projections indicated expansion of *cerrado* and other grassland habitats across the eastern edge of the Amazon Basin (Anhuf et al. 2006), as well as seasonally dry tropical forest (Whitney et al. 2011). Of course, caution must be exercised in stating explicitly where particular vegetation types expanded or contracted, particularly for *cerrado* versus seasonally dry forest (Pennington et al. 2000, Mayle et al. 2004, Pennington 2004), as modern distributions of seasonally dry tropical forest tend to be discontinuous and adjacent to *cerrado* (Mayle et al. 2004). However, given the broad climatic overlap of these two biomes at present, the general pattern of expansion and contraction in response to glacial cycles likely occurred in concert (Prado and Gibbs 1993, Pennington et al. 2000).

Our modeling exercise indicated two possible routes of dispersal for *C. durissus* during the LGM: an Atlantic corridor and a western corridor along the foothills of the Andes. The Atlantic corridor, as reconstructed by both Maxent and GARP, falls in line with current understanding of overall dynamics of the coastal region of northeastern South America during the late Pleistocene. Determining the exact proportions of savannah versus seasonally dry forest will require more palynological and geomorphological data than are presently available (Prado and Gibbs 1993, Colinvaux and de Oliveira 2001, Anhuf et al. 2006, Quijada-Mascareñas et al. 2007, Cowling 2011, Hannah et al. 2011). However, the overarching pattern of change is consistent with periodic establishment of suitable habitat in lieu of favorable climatic conditions as suggested by our models.

The interior (western) corridor along the eastern base of the Andes identified in some of our models was not as well supported as the Atlantic corridor. The extent to which millennial-scale climate events of the Last Glacial cycle were manifested in interior South America remains unclear (Fritz et al. 2010); however, a recent study by Mosblech et al. (2012)

found no evidence of significant drying of the western Amazon Basin in the last 94,000 years. While this result does not instill much confidence, lack of evidence of drying does not necessarily mean that vegetative communities in the region were not impacted by overall drier LGM conditions. In fact, the notion of an Andean dispersal corridor for savannah species during the LIG is not new (da Silva and Bates 2002), so until a better picture of paleoclimates of the South American interior emerges, the potential of an Andean route should not be discarded entirely.

Finally, phylogeographic investigations by Wüster et al. (2005a,b) and Quijada-Mascareñas et al. (2007) found low sequence divergence between *C. durissus* populations north and south of the Amazon Basin, indicating a fairly recent (~1.08 My BP, if molecular clock estimates are to be believed) vicariant event most probably via interruption of a corridor of suitable habitat. Assuming accuracy of this estimation, vicariance of *C. durissus* perhaps coincided with the Mid-Pleistocene Transition (MPT; 1.5 My – 650 Ky BP), a period exhibiting pseudo-periodic moderate climate shifts approximately every 100 Ky (Sepulcre et al. 2011). Despite on-going debate regarding the pattern and extent of vegetation shifts during the Pleistocene, at present no adequate climate data resources exist from which niche models can anticipate mid-Pleistocene distributional responses with any confidence. However, extrapolating from evidence for the more chaotic and extreme Late Pleistocene, MPT climate shifts could have provided windows of optimal conditions stable for long enough to facilitate dispersal from north to south across the Amazon Basin.

The issue of model transferability more generally in ENM studies is an ongoing challenge (Peterson et al. 2007, Owens et al. 2013), and some degree of uncertainty should be expected when projecting spatial and temporal responses of vegetation across time owing to the coarse spatio-temporal resolution (~5 km resolution after downscaling) of paleoclimate reconstructions. A single grid cell at this resolution may often encompass diverse situations (Marchant and Lovett 2011), leading to generalization of conditions. This generalization reduces ability to identify climatically suitable patches at finer extents, thus preventing detection of narrow barriers (Peterson and Nyári 2008). Further, because data available for the LGM and LIG encompass only climatic variables, our models are indicators of climatic suitability only, and do not distinguish directly among vegetation types or other landscape attributes (Nogués-Bravo 2009).

Climate change is a significant factor in the future shifting of plant community structure subsequently impacting the distribution and survivability of most organisms on Earth. Knowledge of the spatiotemporal distribution of species is a major underpinning in understanding the evolution of biodiversity (Svenning et al. 2011). Paleoreconstruction exercises such as the one we present here strengthen understanding of the biogeographic patterns of a given region, enhancing ability to assess "critical" areas more adequately and ultimately playing a significant role in management and preservation of regions such as the *cerrado* and other centers of endemism (da Silva and Bates 2002, Varela et al. 2011). Exploration of model-based scenarios for many taxa in relation to critically, non-model-based studies (genetic, paleo-environmental studies, etc.), provide a form of "ground-truthing" for the model-based results. By identifying most parsimonious scenario(s) of species' and community

responses to past climate changes, we improve ability to develop and implement more effective, long-term management strategies in the face of projected future climate scenarios.

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