



Phylogeography is not enough: The need for multiple lines of evidence

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The concepts of equilibrium and stability in biogeography are perhaps much more fleeting than has generally been appreciated, and disequilibrium may actually rule the situation in most cases (Manning et al. 2009). That is, although researchers may discuss current distributional patterns as fixed, those patterns may have been in place only for a relatively short period of time ($\sim 10^4$ yr), perhaps since the last major global cool period at the end of the Pleistocene (Figure 1). Although Pleistocene climatic fluctuations have been considered a major force in biogeography, and some have argued that they may have produced much of current species diversity (Mengel 1970, Haffer 1997), the validity of the Pleistocene speciation paradigm has been debated hotly recently—see, e.g., Klicka and Zink (1997) versus Weir and Schluter (2004).

“The Pleistocene” is often cited as a biogeographic force, but too often uncritically and without full consideration of the complexity of world climates over the past million years. That is, molecular systematists frequently use molecular “clocks” that date splitting events imprecisely, usually with confidence intervals so broad as to inspire concern (Peterson 2007); these studies often refer to Pleistocene climatic fluctuations, but with no specifics, although the ability to date splitting events may improve with broader use of population-genetic approaches to the challenge (Arbogast et al. 2002). This general appreciation of the role of Pleistocene climatic fluctuations as important biogeographically nonetheless has not to

date translated into detailed analyses of key events structuring biogeographic patterns in many phylogeographic analyses.

In particular, the Pleistocene was characterized by a complex series of warm periods (similar to present-day climates) and cold periods (“ice ages”), with impressively short transitions in between (Figure 2; Dansgaard et al. 1993). Although considerable attention has focused on the last of the glacial maxima ($\sim 21,000$ yr before present), in reality, all of these alternating periods of warm and cold climates probably had some influence on present patterns of diversity and distribution of biodiversity (Svenning and Skov 2004). The purpose of this commentary is to reflect on likely effects of such repeated and dramatic global climate fluctuations in shaping patterns of distribution of species, and to emphasize the need for broader

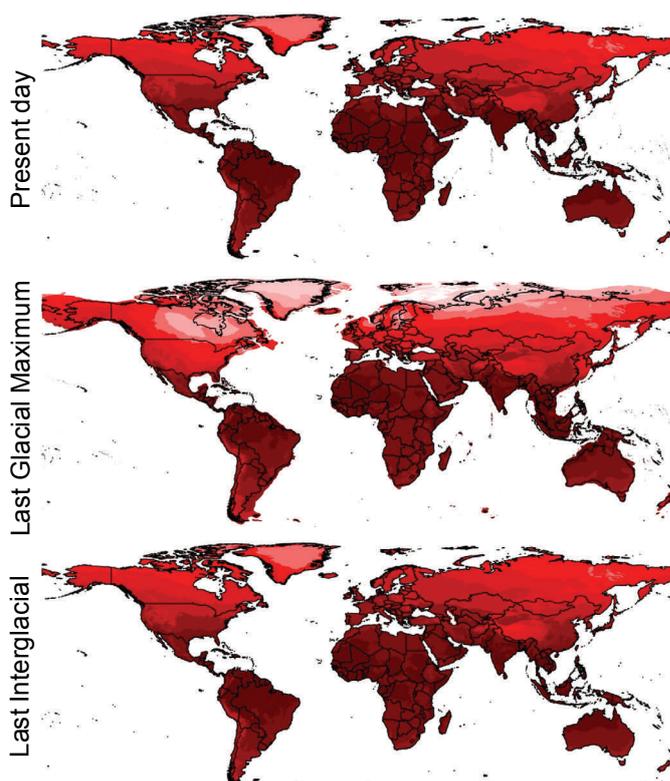


Figure 1. Temperature and precipitation fluctuations over the past 135,000 yr: shown are annual mean temperature profiles (all on the same scale) for the present day, Last Glacial Maximum (21,000 yr ago; CCSM scenario), and Last Interglacial (135,000 yr ago; Otto-Bliesner et al. 2006). The 10 shading classes cover equal intervals between -50° and $+31.5^\circ\text{C}$.

analyses aimed at clarifying the roles of these effects in biogeographic studies.

Why are species where they are? The BAM diagram

Soberón and Peterson (2005) presented a framework for understanding geographic distributions of species that considers autecology, synecology, and geography (Figure 3). That is, following the earlier framework of Hutchinson (1978), they envisioned the broad, climatically determined abiotic (“fundamental”) niche as being reduced to some degree by biotic interactions necessary for the species’ persistence in a region to create a “realized” niche that emphasizes the role of negative interactions in reducing species’ ecological potential. However, Hutchinson (1978) neglected effects of geographic heterogeneity and subdivi-

sion and limited dispersal, and as such missed quite a bit of complexity that has been the focus of historical biogeography. The Soberón and Peterson (2005) framework thus included considerations of movement and access as a further constraint on the distributional potential of species. This combination of aspects of Biotic interactions, Abiotic conditions, and Movement (hence “BAM”) outlines major factors affecting the distributional potential of species.

The basic BAM configuration (Figure 3), however, is not necessarily representative of particular cases. Rather, other BAM configurations are possible (Figure 4): these configurations likely correspond to the mental pictures that different suites of researchers may have regarding species’ distributions. For example, the classic “community ecology” viewpoint (similar to Hutchinson’s ideas) would paint **M** as broad, but $\mathbf{A} \cap \mathbf{B}$ as quite restrictive, thus emphasizing the role of interactions among species in determining species’ geographic potential. The biogeographer, on the other hand, imagines that $\mathbf{A} \cap \mathbf{B} \approx \mathbf{A}$; under this view, biotic interactions may not affect abiotic potential dramatically (at least at coarse-grained resolutions; Soberón 2007), and rather a restrictive **M** determines the key features of species’ distributions—note that this configuration coincides with recent trends towards downplaying the role of local biotic interactions in structuring ecological communities (e.g., Ricklefs 2008). Although the degree to which the community ecologists or the biogeographers are correct across major swaths of biological diversity has not been resolved, and must remain a topic for future research, these viewpoints probably represent extremes of the set of likely possibilities.

The critical role of M

The above discussion of the BAM diagram points toward a key role of dispersal limitation in shaping species’ geographic distributions. In particular, **M** is determined by some combination of present-day dispersal ability (e.g., capacity for movement between natal and reproductive sites), and historical range shifts that opened access to areas relatively more remote from present-day distribu-

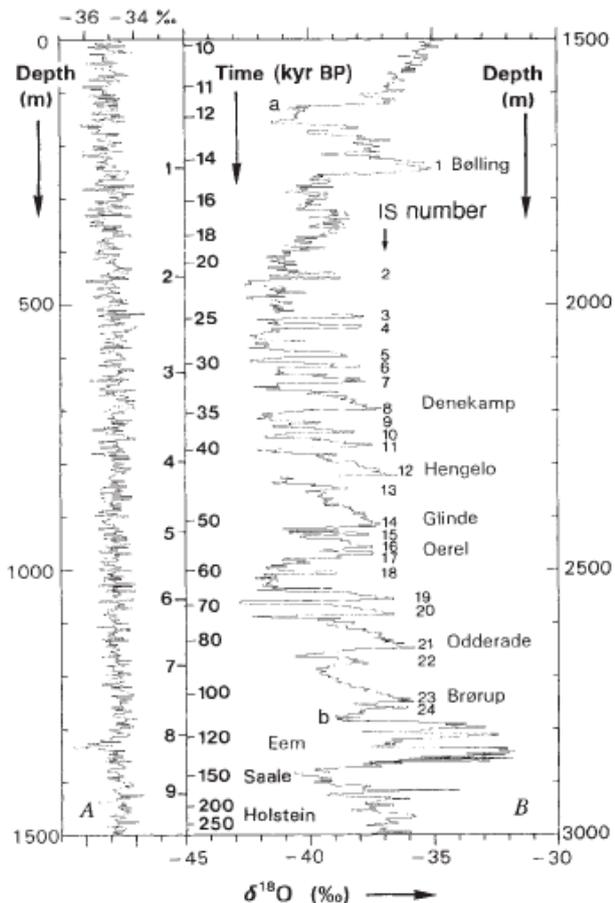


Figure 2. A continuous $\delta^{18}\text{O}$ record plotted in two sections on a linear depth scale: (A) from surface to 1500 m, and (B) from 1500 to 3000 m. Each point represents 2.2 m of core increment, and glacial interstadials are labeled at the right. Figure reproduced from Dansgaard et al. (1993), who also provide further detail.

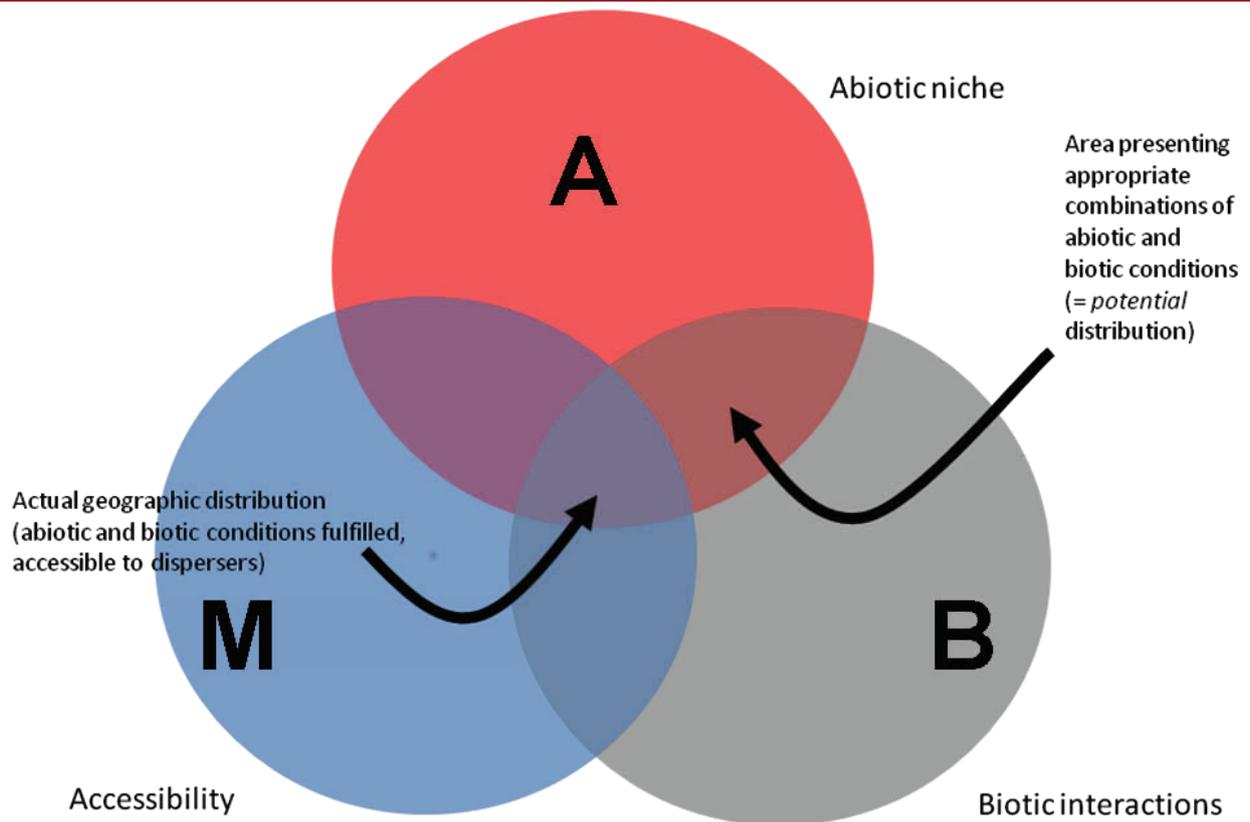


Figure 3. The “BAM diagram,” showing a simplified framework for understanding where species will and will not be distributed. Distributions of species are seen as responding to three sets of factors: the abiotic niche (**A**, in red) and the biotic niche (**B**, in gray), which roughly correspond to the fundamental ecological niche (**A**) and the realized ecological niche ($A \cap B$, here termed the potential distribution) of Hutchinson (1978). A further modification to distributional potential, however, is that of accessibility (here **M** for “movement,” in blue), which may constrain species’ distributions dramatically. Reproduced from Soberón and Peterson (2005).

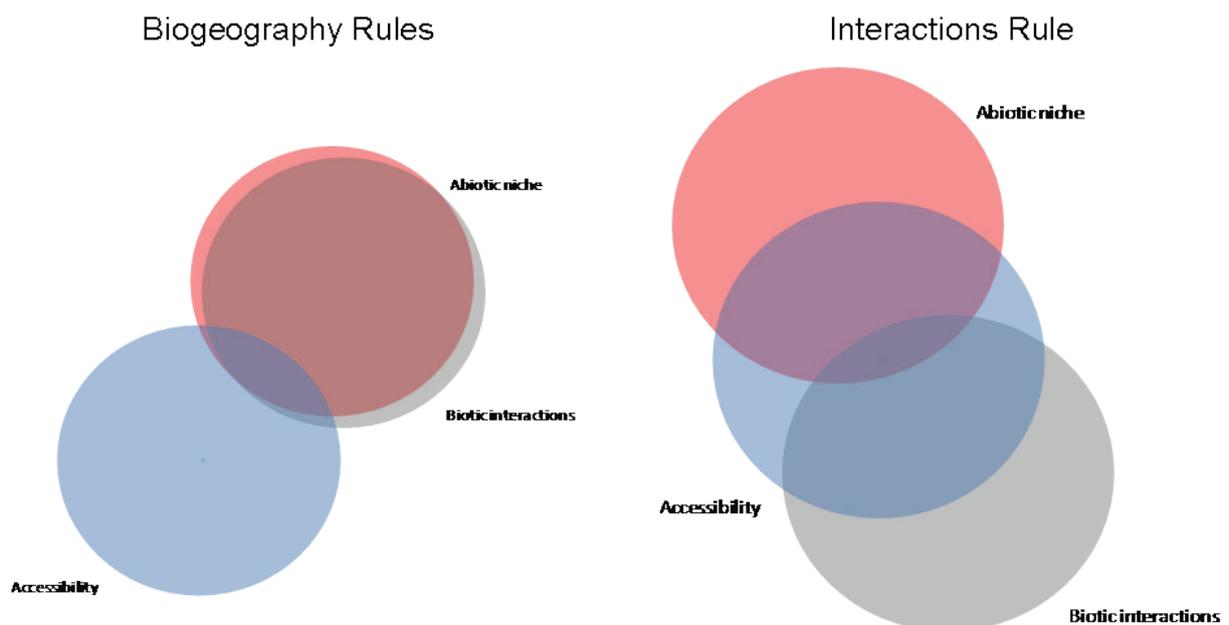


Figure 4. Different configurations of the BAM framework that emphasize different factors. Left side: abiotic and biotic considerations overlap broadly, permitting neglect of biotic effects in reducing abiotic potential, but accessibility is constrained, perhaps owing to a highly subdivided biogeographic landscape. Right side: accessibility is quite broad, but abiotic and biotic conditions necessary for survival are very restrictive, indicating a situation in which biotic interactions modify abiotic potential substantially.

tional areas (Soberón and Peterson 2005). The importance of the latter phenomenon is evidenced by the frequency of relictual isolated populations in many parts of the world (e.g., Smith et al. 2000).

In the context of this commentary, historical components of **M** frequently have been imposed by “hard” barriers (i.e., barriers that do not shift with changing climatic conditions), including shorelines, large rivers, mountain ranges, deep valleys, and other topographic features. These features, at least in general, have remained largely fixed even as major climatic shifts have occurred, for example over the past million years, with the

Pleistocene glaciation events. To the extent that species were unable to disperse across such barriers, the availability of particular climatic conditions in particular biogeographic regions may be restricted dramatically during certain climatic events (see, e.g., Figure 5). These dynamics may have dominant influences on which species are able to survive, and in what numbers, in a particular area.

Pleistocene climatic fluctuations

The influence of the dramatic Pleistocene climatic fluctuations on distributions of species needs to be considered in the framework just presented. That is, given the constraints of **M**, a species should persist only in areas that are simultaneously suitable environmentally and accessible over the long-term integration of these climate-change processes. One can imagine the spatial representation of a particular species’ niche in a region defined by hard barriers through time—if that representation becomes too fragmented or too reduced, then the species will not be likely to persist there.

A further constraint is that of distributional disequilibrium within **M** (Svenning and Skov 2004, 2007). That is, Pleistocene climatic fluctuations likely frequently produced spatial shifts in habitable areas within areas delimited by hard barriers. To survive a period of change, the species must have dispersal abilities sufficient to track the habitable areas sufficiently quickly such that it is not left behind (Holt 1990), without being able to reach habitable area even within the region defined by the hard barriers. That is, even if the hard-barrier-defined region retains suitable areas, the species must nonetheless be able to track those suitable areas as they shift to be able to survive in the area in the long term.

If conditions change very rapidly, as might have been the case in the Pleistocene (Figure 2), spatial shifts of suitable areas may overcome the dispersal and colonization abilities of the species. In this case, species may be able to persist only via refugial populations in specific areas remaining habitable in the region through climate changes. That is, when climate change is extremely rapid,

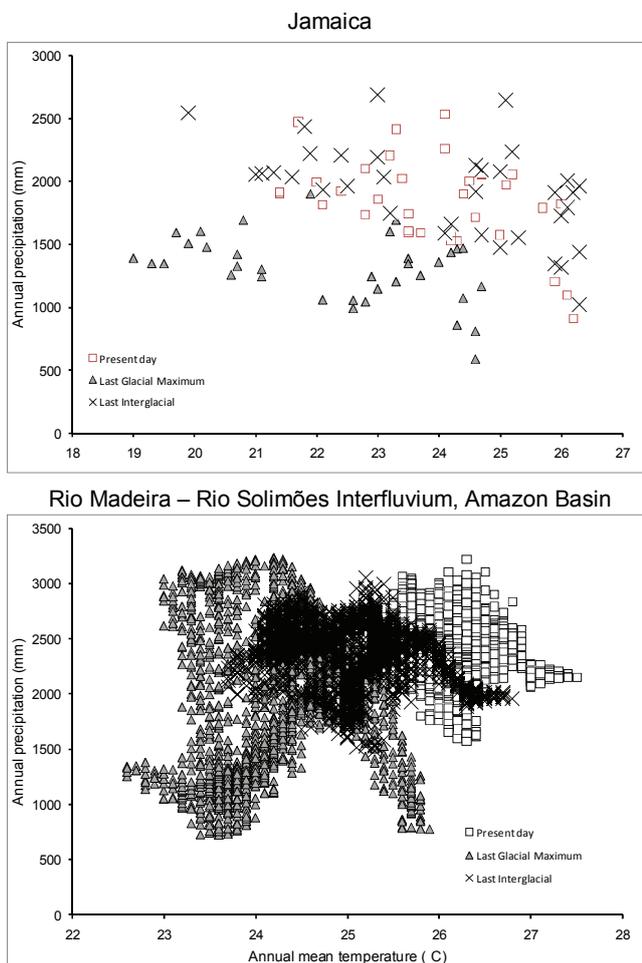


Figure 5. Examples of effects of geographic constraints on manifestations of ecological conditions: temperature and precipitation variation over the past 135,000 yr in Jamaica and in the Rio Madeira – Rio Solimões interfluvium in the Amazon Basin. The paleoclimate data are from the CCSM climate model (Collins et al. 2004), and the points represent grid cell values across the region at 0.17° resolution. Note the partial overlap between conditions in different periods in both regions.

species' dispersal abilities may not allow tracking the shifts in suitable areas, but persistence may be possible in areas of overlap between warm- and cold-condition suitable areas. These refugial areas may thus provide the key to persistence when conditions change particularly rapidly.

Beyond phylogeography

The discussions above point out that persistence of species in regions characterized by hard barriers is a delicate and constrained phenomenon when climates change dramatically. This situation was manifested particularly frequently in the Pleistocene, when global climates switched between warm and cold climate conditions rapidly at many points. This dynamic likely affected major portions of global biodiversity during much of the last million years of Earth history.

Phylogeography at its roots is a cross-linking field, intended to touch multiple fields and multiple suites of tools (Avice 2000), and some phylogeographic research has indeed reached out in more diverse directions. The scenarios of rapid change and perpetual disequilibrium discussed herein suggest, however, that common practice phylogeographic and molecular ecology approaches to biogeography will frequently prove inadequate to capture the details of the biogeographic history of lineages. Imprecise dating of key splitting events means that typical phylogeographic approaches will come up short in explaining Pleistocene biogeography, referring only indefinitely to time spans that cover multiple warm or cold periods. They will paint a general picture that too frequently consists of generalities only, and cannot anticipate the fine details.

In addition, phylogeographic approaches have no means by which to address the "where" of biogeographic events. Phylogeographic breaks have a known position at present, but that position may or may not correspond to the position of the break, or the geographic feature that caused it, in the past. Coalescent approaches may indicate population expansion or relictual distributions, but cannot inform as to where those populations were located when they were large or small.

Multiple lines of evidence will be necessary to clarify this situation, i.e., phylogeography needs company in meeting the challenge of understanding the past geography of biodiversity. The field that could be termed "species-level quantitative distributional ecology"—often referred to as ecological niche modeling—offers an opportunity here (Soberón and Peterson 2004). That is, niche models trained and validated under present-day conditions can be projected onto past conditions corresponding to specific points in the past—currently, paleoecological scenarios are available for 6000, 21,000, and 135,000 yr before present (Hijmans et al. 2005a, b). Hindcasting (i.e., retro-projections of present-day niche models) permits development of explicit paleodistributional scenarios to which phylogeographic patterns can be compared via coalescent simulations, potentially permitting testing explicit hypotheses of causation by particular climatic events. What is more, the explicit geographic hypotheses that are developed provide the potential for estimates of ages of lineages independent of the imprecise clock-based estimates customarily employed.

Studies to date have confirmed ecological niche conservatism over the latter part of the Pleistocene (Martínez-Meyer et al. 2004, Martínez-Meyer and Peterson 2006, Banks et al. 2008), and have indicated significant predictive ability of paleodistributional predictions of niche models regarding phylogeographic patterns (Peterson and Nyári 2007, Waltari et al. 2007, Waltari and Guralnick 2009). Niche modeling approaches, however, still have many hurdles to overcome: for example, serious conceptual and methodological issues remain in the realms of niche estimation (Soberón 2007), model interpretation and thresholding (Pearson et al. 2007), and model validation (Lobo et al. 2008, Peterson et al. 2008). Even more importantly, the challenges of transferring niche models among very different environmental landscapes (e.g., from present-day to Last Glacial Maximum) are only beginning to be explored—complications include the coarse grain of present-day paleoclimatic data sets, error and inaccuracy in those same data sets, and the question of how conservative are ecological niches

through evolutionary time, so many important lessons remain. An important specific step will be development of multiple paleodistributional hypotheses corresponding to different time periods, with quantitative comparisons of their explanatory abilities regarding different “slices” of the evolutionary history of the group (Carstens and Richards 2007, Knowles et al. 2007).

More generally, the availability of powerful, quantitative tools in phylogeography and biogeography should be an impetus towards greater rigor in the field. That is, molecular approaches provide fascinating views into the population genetic past of lineages; their results, however, are limited for lack of spatially explicit inferences, so other sources of information are needed. Ecological niche modeling and their projections onto paleoclimatic scenarios offer one important means of enriching these views into the past. These multiple lines of evidence will provide a much richer view of biogeographic history, as has become evident from the success of first steps in this direction (Carstens et al. 2005, Cheddadi et al. 2006, Carstens and Richards 2007, Knowles et al. 2007, Peterson and Nyári 2007, Alsos et al. 2009, Waltari and Guralnick 2009).

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