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update

Recent advances in using species distributional models to understand past distributions

The first wave of climate-driven, paleoecological, species distribution models (SDMs) focused primarily on testing global climate models (GCMs; e.g., Bartlein et al. 1986). Recently, a second wave of research, using increasingly sophisticated SDMs, expanded the use of paleo-SDMs into biogeographic questions. This new focus is contributing substantially to discussions about outstanding questions in biogeography, such as stability of niches through time and fundamental spatiotemporal controls on geographic patterns of biodiversity.

The value of paleo-data in biogeographically oriented distributional models gained prominence when Nogués-Bravo (2009) highlighted the use of SDMs for investigating past distributions of species. Nogués-Bravo (2009) outlined areas where paleo-data can help understand and test some of the assumptions underlying SDMs, highlighted methodological considerations when creating and projecting SDMs through time, and recommended a set of best practices when extending SDMs to include paleo-data. Since then, many new studies have utilized paleo-SDMs, alone or in combination with other approaches, and the number of papers relying on paleo SDMs has grown rapidly (e.g. 27 studies reviewed by Nogués-Bravo 2009; 82 studies reviewed by Svenning et al. 2011). Two recent review papers (Svenning et al. 2011; Varela et al. 2011) deepen the discussion about paleo-SDMs by synthesizing this new research, discussing advances made in paleo-biogeography, and outlining the challenges going forward. While there are many points of agreement between the two reviews, reading them in parallel makes obvious some areas of disagreement that point to unresolved issues with paleo-SDMs.

SDMs based on modern distribution data are influenced by a number of different uncertainties, including incomplete distribution information, simplified or uncertain mechanistic relationships between distribution and climate, and extrapolation into no-analog climates, to name a few (e.g. Guisan & Zimmermann 2000; Guisan & Thuiller 2005; Elith et al. 2006; Jiménez-Valverde et al. 2008). Paleo-SDMs are subject to the same limitations, but often to a greater extent. Many of these technical issues are discussed in detail by Varela et al. (2011), with the goal of establishing a "robust and scientifically-based theoretical and methodological framework" for the use of SDMs in paleobiology. They focus largely on the particulars of paleontological data, and highlight issues of spatial, temporal, taphonomic, and collection bias that should be considered when modeling and interpreting paleo-SDMs. Varela et al. (2011) advocate cautious use of paleo-SDMs, arguing that paleo-SDMs are promising but that key gaps in knowledge currently limit their widespread application.

The use of SDMs in paleobiology has grown rapidly despite these limitations. Svenning et al. (2011) synthesize the many ways that SDMs have been and could be applied to outstanding questions in paleoecology. Their review is broader (82 papers vs. 42 reviewed by Varela et al. 2011) and focuses in particular on the integration of SDMs with genetic data. They outline four primary applications of SDMs, including the use of paleo-SDMs to test hypotheses about glacial refugia, the end-Pleistocene megafaunal extinctions, Holocene paleoecology, and deep-time biogeography. Svenning et al. (2011) provide a more optimistic view of the use of SDMs in paleobiology, perhaps because they focus more on applications of paleo-SDMs and less on potential issues with the underlying data.

However, some recommendations by Varela et al. (2011) imply that work highlighted by Svenning et al. (2011) should not be attempted at large spatial or temporal scales at this time. As one example, both groups correctly argue for caution when using and interpreting statistically-downscaled climate simulations. However, Varela et al. (2011) take a highly conservative approach and argue that statistical downscaling should not be used because extrapolating current climatic anomalies into the past may lead to error; they recommend waiting for wider availability of regional climate models to downscale GCM simulations. This would preclude many of the continental to global paleo-analyses advocated by Svenning et al. (2011), such as identifying cryptic glacial refugia across Europe, at least until regional climate models are widely available. Related to this issue, the hypothesis-testing framework of Svenning et al. (2011) may be sensitive particularly to the choice of GCM. The influence of different climatic reconstructions on paleobiogeographic patterns is not discussed in depth by either review. Highlighting inconsistencies between paleoclimate models and fossil data is an important contribution that paleobiogeography continues to make to paleoclimatology (e.g. Bartlein et al. 2011).

One other issue that merits additional discussion is the use of abundance data in paleo-SDMs. Varela et al. (2011) recommend against using abundance in paleo-SDMs and abundance data are not often used in neo-SDMs either (but see, e.g., Huntley et al. 2012). Although not explicitly stated, the perspective of Varela et al. (2011) seems influenced by vertebrate fossil remains, which often are deposited discontinuously. However, some paleo-proxies, such as continuously deposited microfossils with large sample sizes and constant taphonomic regimes (e.g. pollen, ostracods, foraminiferans, diatoms), have a strongly established tradition of using abundance data, which may also be appropriate for use in paleo-SDMs. Such abundance data could, with caution, be used to investigate range shifts, leading edge/trailing edge dynamics, and relationships between migration and climate velocity, for example.

Overall, the explosion of paleo-SDM research represents a shift in how space and time are integrated to tackle biogeographic questions. The two recent reviews provide a cautious but exciting measure of the maturity of the field. There are ongoing areas of discussion about appropriate use of paleo-SDMs that would benefit from close collaboration between biogeographers, paleoecologists, and climate modelers. Given the integration of SDMs with other lines of evidence such as fossil and genetic data, paleobiogeographers are now able to provide much more detail and sophistication to many of the hypotheses outlined by Svenning et al. (2011).

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