



# Conservation paleobiogeography: the past, present and future of species distributions

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We have long known that the past can inform the future (Dietl and Flessa 2011), but in the field of conservation paleontology, models of current and future situations also inform how we study the past, providing frameworks and hypotheses to be tested using historical experiments. The information provided by the fossil record is used to build and calibrate the models that we use to predict the future. Because information flows in both directions, conservation paleontology is a powerful tool for addressing complex biogeographic issues, such as predicting species distribution patterns under alternate climate regimes. In trying to understand distribution patterns, conservation biology and paleontology ask very similar questions. For example: What is a species' fundamental niche? Do fundamental niches evolve as the environment changes? How do interspecific interactions affect how those niches play out on the landscape? These disciplines use many of the same tools: niche reconstructions, niche conservatism metrics, and species distribution projections (forecasts or hindcasts). In the process of answering these questions, conservation biologists and paleontologists are synergizing to advance the field of predicting species distribution patterns all the more rapidly.

Figure 1 depicts the challenges that practitioners face when trying to predict species distributions. Many methods are available both for estimating the fundamental niches of species and for projecting those niches onto geographic map space to determine species distributions (Fig. 1; see Peterson et al. 2011 for an exhaustive volume on concepts and methods). Both steps in this process are a major challenge. The fundamental niche is defined by Hutchinson (1957) as the set of environmental variables at which positive population growth can be maintained. An active debate also exists over how to most accurately estimate a fundamental niche. Conservation paleobiogeographers estimate the fundamental niche using methods ranging from correlative (McGuire and Stigall 2009, McGuire and Davis 2013) to mechanistic (Allen et al. 2010, Pound et al. 2011, Prentice et al. 2011). However, regardless of how one has estimated a species niche, we face similar challenges when trying to project that niche onto the landscape (Fig. 1 right panel). Although there are nuances, three types of challenge restrict

species distributions even more than the limits of their fundamental niches: interspecific interactions, dispersal limitations, and disequilibrium or historical contingencies (Fig. 1; Peterson et al. 2011). Occasionally, there may also be situations where a species distribution strays outside of its fundamental niche, for example in the cases of facultative interactions or sink populations (Fig. 1).

With all of these various environmental and biotic stressors acting on the populations of interest, one can see that the populations should evolve over time. In theory, the stronger the stress or the more evolvable the species, the more rapidly their fundamental niche will change. As a result, the entire set of geographic regions where that species could theoretically live would shift. A long-standing suite of questions in the field concern niche conservatism through time. At what taxonomic or temporal scale does niche conservatism occur? In what situations do we find increased or decreased niche conservatism?

In January 2013, at the biennial meeting of the International Biogeography Society in Miami, FL (Dawson et al. 2013), we brought together a group of researchers working on progressive aspects of conservation paleobiogeography in a symposium entitled “The Convergence of Conservation Paleontology and Biogeography.” Several of their research projects are included in this special issue of *Ecography*. Each of the papers herein explores the interactions between environmental variables and species niches that will enable more accurate projections of species distributions onto the landscape in past, present and future climates. Importantly, they integrate the tools and methods used in conservation biology and paleontology in such a way that simultaneously addresses outstanding hypotheses and progresses methodologies that will be used to predict past and future species distributions.

## Innovation

Davis et al. (2014) demonstrate the challenges depicted by Fig. 1 by examining the accuracy with which basic correlative ecological niche modeling (ENM) methods

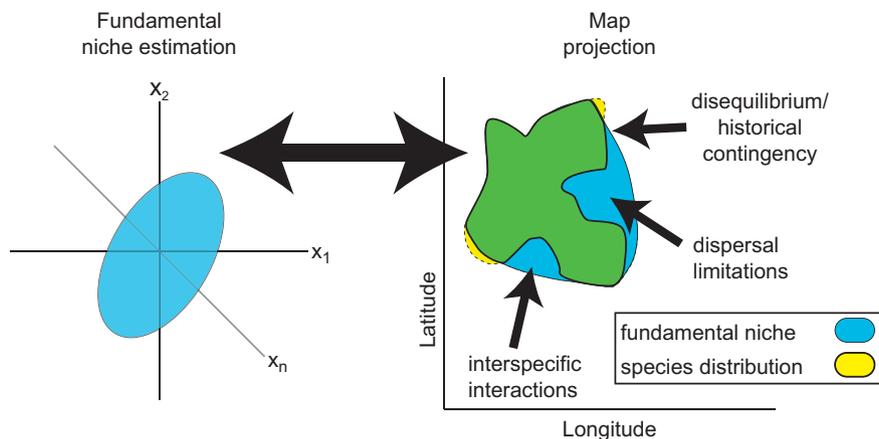


Figure 1. When predicting a species distribution, the fundamental niche of the group of interest is estimated (left panel) and then that niche is projected onto a map (right panel). Correlative niche estimation methods use occurrence data (where individuals are found on a map; left panel) to estimate the fundamental niche (right panel). When the fundamental niche estimate is projected onto geographic space, it is further limited by interspecific interactions, dispersal limitations, and disequilibrium or historical contingencies to form the actual species distribution on the landscape. In some cases the species distribution may exceed the fundamental niche space, such as in cases of facultative interactions or sink populations.

project species distributions during a much colder climate, the last glacial maximum (LGM). Davis et al. test how well hypothesized LGM distributions for a group of small mammals align with empirical fossil localities and discover a consistent southerly bias in the ENM distribution hypotheses, a result that confirms work by Guralnick and Pearman (2010). The original analysis tested by Davis et al. (2014) estimates each species' niche using their modern geographic distributions, creating a realized niche that was then projected back onto a LGM climate surface (Waltari et al. 2007). Davis et al. (2014) point out that any of the reasons enumerated in Fig. 1, in addition to poor paleoclimate data, could be the source of the consistent bias in their results.

Another issue that is not addressed in depth in Davis et al. (2014), but that has important implications for projecting niches onto species maps is that of environmental data extrapolation. Varela and others perform an important study found in this issue that explores how environmental versus geographic sampling affects the accuracy of ENMs. Varela et al.'s (2014) findings will change the way practitioners are performing ENMs. Until now, it has been the norm to evenly geographically sample specimens that are used to train ENMs and estimate niches, but Varela et al. (2014) demonstrate that this practice can bias niche estimations, and subsequently, the map projections (Fig. 1). Therefore, when estimating a species niche, it is best to evenly sample environmental data, especially if dealing with a relatively small sample size (Varela et al. 2014).

Both Davis et al. (2014) and Varela et al. (2014) deal with correlative methods for estimating species niches. An increasingly popular and necessary method to estimate niches is through mechanistic methods. Although they do not explicitly deal with distribution models, the paleoecological data provided by Tovar et al. (2014) is exactly what is necessary to examine the strength of mechanistic biodiversity distribution models through time. Tovar et al. (2014) compared burn patterns in central African rainforests.

They demonstrate that human burn patterns rather than previously suspected climate patterns drive the distributions of particular forest types. Were one to model these forest distributions, it would be imperative to incorporate burn patterns and human activities as a variable.

Another important way to improve species distribution predictions is to learn how interspecific interactions, dispersal limitations, and historical factors affect niche projection onto the environmental landscape. Blois et al. (2014) establish a thorough framework to analyze species associations to determine the relative roles of interspecific interactions, dispersal, and their associations with environmental variables. To create this framework, they first test species co-occurrences using a null-model analysis and then analyze environmental signals in the significantly associated species pairs. To demonstrate the utility of their framework, Blois et al. (2014) use a substantial genus-level pollen dataset from the late Quaternary of eastern North America and derived from the Neotoma Paleocology database ([www.neotomadb.org](http://www.neotomadb.org); Blois et al. 2011). They find relatively very few significant species associations through time, even fewer of which seem to have a strong interspecific interaction signal (Blois et al. this issue). These findings may be early indicators that interspecific interactions do less to limit species distributions than we might suspect (Fig. 1).

Looking at interspecific interactions over a much deeper timeframe, Stigall (2014) traces niche stability by examining a suite of invertebrates through six stratigraphic sequences of the Late Ordovician (~ 450 Ma). She finds that niches generally experience stasis during periods of moderate environmental change, but that they undergo relatively dramatic shifts during periods of biotic interchange (Stigall 2014). This implies that distribution models should have relatively accurate transference through time given similar environmental conditions. However, it reinforces the idea that interspecific interactions may be very important components to incorporate into distribution models if we are to attain accurate predictions.

Integrating a deep time component to species distribution research can also reveal how conserved fundamental niches are by tracing their change through time. This time-transgressive approach allows researchers to explore the evolvability of a taxon when faced with specific physiological pressures. Lawing and Matzke (2014) review the progress that has been made integrating phylogenetic thinking into estimating species niches and predicting species distributions through time. They establish an ambitious conceptual framework of methodological advances necessary to more accurately reconstruct species niches and more fluidly move between niche space and projected map space. They point out that when the data are available one should strive to integrate as much physiological, phylogenetic, and paleontological data into ENMs as possible to achieve the best reconstructions. If it proves necessary to innovate new methods to integrate these data, it is worthwhile and progresses the field.

## Moving forward

ENMs were initially all about predicting species distributions (Guisan and Zimmermann 2000), and although this is an important question still today, this is no longer the entire focus of the field (Peterson et al. 2011). Because we realize that so much complexity goes into projecting niche estimations onto maps, researchers have been innovating ways to more fluidly transition between niche space and map space (Fig. 1; Warren et al. 2010, Varela et al. 2011). These methods are important for assessing questions such as, “How broad is the realized environmental space?”, “How well does the realized niche approximate the fundamental niche?” and “How much has the fundamental niche changed through time relative to the realized environmental space?” In answering these questions, not only are we progressing a method that is critical for conservation purposes, we are also addressing core questions to biogeography. Several of the papers in this issue add to the growing body of techniques that increases methodological flexibility and improves our understanding of the complex interplay of realized niches, fundamental niches and species distributions (Blois et al. 2014, Lawing and Matzke 2014, Stigall 2014, Tovar et al. 2014, Varela et al. 2014).

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