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Ecological niches and present and historical geographic distributions of species: a 15-year review of frameworks, results, pitfalls, and promises

A. Townsend PETERSON and Tashitso ANAMZA

Biodiversity Institute, The University of Kansas, Lawrence, Kansas 66045, U.S.A.; e-mail: town@ku.edu

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Abstract. We present an overview of the emerging field of species-level distributional ecology, particularly as it relates to phylogeographic studies of birds in Eurasia. This field centers around distributional inferences and predictions deriving from the use of ecological niche modeling. We provide a brief historical review, and then proceed to outline a number of crucial methodological considerations, if models are to have biological meaning and reality. We then proceed to provide a worked example, as well as some thinking about directions in which the field should be moving in terms of questions and approaches.

Key words: distribution, ecological niche, phylogeography, Pleistocene

Background

The general idea of understanding geographic distributions of species via exploring their environmental requirements is about a century old now, having begun with explorations by Joseph Grinnell in the early 1900s (Grinnell 1917, 1924) – Grinnell, in effect, laid out much of the idea of the ecological niche that is central to many contributions in ecology and biogeography today. Grinnell's approach centered on comparing environments manifested within species' distributional areas with those manifested outside of distributional areas to establish which environments are required for the species' persistence in an area. Grinnell also appreciated the roles of other factors not related to environmental requirements, such as barriers to dispersal, which nonetheless modify distributional potential of species (Grinnell 1914).

It must be borne in mind that, at about this same point in history, the "New Synthesis" of evolutionary biology was just initiating, in which ideas from genetics and ideas from evolutionary theory were first integrated (Mayr 1942). As a consequence, perhaps we should not expect a full, synthetic view linking geography, ecology, and evolution from Grinnell. That viewpoint took several decades to evolve, with important early papers by evolutionary geneticists including Sewall Wright (Wright 1943, 1982) and others. Still, Grinnell's view was among the very first to link geography with ecology, such that he took important first steps.

In a much more modern context, Avise (2000) provided initial linkages between patterns of differentiation of molecular genetic characters across real-world landscapes. This now well-established field – phylogeography – has achieved excellent synthesis in its basic mission: how large numbers of diverse molecular characters evolve through history across distributions of species. This broad achievement is well illustrated by the table of contents of this special issue.

Where the field of phylogeography has perhaps not been as successful or as deeply incisive is on the "geography" side of the equation (Peterson 2009). That is, whereas the field has entered deeply into how genes and lineages evolve, and when lineages can and should be considered as independent, it has not interfaced as intimately with the geographic landscape over which these processes are occurring. Certainly, exceptions are emerging, in which incisive and creative analyses are getting to deeper levels of synthesis linking phylogenetic and phylogeographic pattern to landscapes (Carstens et al. 2005, Carstens & Richards 2007, Edwards et al. 2012). The broadest and deepest of levels of synthesis, however, are perhaps still just over the horizon for this field.

After Grinnell

In the past couple of decades, approaches derived from Grinnell's general paradigm have become quite popular in ecology and biogeography, taking advantage of rich lessons to be gained from understanding species' environmental requirements (ecological niches) and how they translate into distributional limitation. Specifically, parameters of fundamental ecological niches (N_F, the set of environmental conditions within which the species is able to maintain populations without immigrational subsidy) are estimated via examination of associations between known distributional patterns and environmental variation across regional landscapes; these so-called "correlational ecological niche models" (hereafter "ENMs") have become extremely popular, and now appear in publications in diverse fields.

Regarding the themes that are the focus of this special issue, these methodologies have excellent promise in (1) estimating distributional potential of species, (2) assessing distributional continuity across landscapes, (3) evaluating whether environmental requirements of species (niches) have differentiated as populations diverge and diversify, and (4) offering explicit hypotheses of past potential distributional patterns (e.g. under conditions at the Last Glacial Maximum). As such, this general approach shows considerable promise as a complement to the more traditional phylogeographic toolkit, which focuses more in the realms of population genetics and phylogeny. The ENM approach, in effect, offers to phylogeography the sister dimensions of space and environment as additional key parameters with which to describe and understand the dynamics of distribution and differentiation of populations of evolving species.

Still, amidst this promise, ENM approaches see considerable abuse and misuse – that is, as these tools have become easier and easier to apply, they have been applied in situations in which they are not applicable, and their outputs have been interpreted in ways in which they should not be interpreted (Peterson & Soberón 2012). Getting to the interesting and useful biological insights, without falling into the methodological traps, is the crucial trick in getting the most out of these new tools. The aim of this review is thus to guide potential users of these tools toward interesting and exciting applications, while at the same time avoiding the mistakes and pitfalls that are strewn along the path. We illustrate our points with the example of the great tit (*Parus major*), a species for which phylogeographic data have been developed, and that is rather emblematic of geographic variation and population differentiation across Eurasia.

The BAM framework

Although Grinnell's early ideas focused on requirements of species with respect to coarse-resolution, "abiotic" environmental parameters, he clearly was aware that other factors enter the picture, including aspects of interspecific interactions (Grinnell 1917) and limitations to dispersal (Grinnell 1914). Hutchinson (1957) championed and built the "niche" picture quite a bit more, and emphasized effects of interactions with other species, but neglected the dispersal picture almost entirely. Indeed, a more balanced picture of the niche-and-distribution phenomenon did not appear until Pulliam (2000), which was made more explicit and restated as the so-called "BAM" diagram by Soberón & Peterson (2005).

Here, we introduce some formality and notation into the discussion, to permit clarity in discussions of key concepts: in general, boldface will be used to indicate sets, and enclosing items in parentheses indicates operations to be applied to those items. The BAM framework posits that distributions of species are manifested in two linked spaces (Soberón & Nakamura 2009): G, for geographic space, and E, for multivariate spaces of environmental conditions (see Fig. 1 for an example of these two spaces). Notational conventions are used to translate between the two spaces: $\eta(X)$ indicates the environmental conditions associated with some geographic location X, and $\eta^{-1}(Y)$ refers to the geographic locations associated with some set of environmental conditions Y. With this basic terminology, it is possible to describe distributions of species manifested in these two linked spaces.

Distributions in G represent a three-way interaction among distinct suites of factors. That is, whereas N_F lays out a basic set of habitable areas for a species, which is referred to as A, that area may be reduced (or even expanded) by biotic interactions; the area that is habitable by the species in terms of biotic considerations is called B. What is more, species do not have universal and all-reaching dispersal abilities: the areas that have been accessible to the species over relevant time periods are termed M. Finally, and more in methodological and empirical realms, not all areas have been sampled by scientists, such that only an area (termed S) has any possibility of providing occurrence records of the species (termed G_+) for analysis, and some areas will provide many more records than others. The area $B \cap A \cap M$ represents the area where populations of the species can be maintained (termed the occupied geographic distribution, or G_O), and the area $B \cap A \cap M \cap S$ is the area from which occurrence records (termed G_+) can come. Note that the area $B \cap$

A will generally be broader, and can be termed the potential geographic distribution, or G_P. Most likely, M considerations dominate at the coarsest scales (e.g. all life known so far is dispersal limited to Earth, and has not colonized to or from other planets, much of biodiversity is structured by continents, etc.); A likely dominates at somewhat finer scales, with climatic tolerances setting many range limits within broader continents; and B probably acts chiefly at fine scales that perhaps can be neglected in studies focused on biogeography (Soberón 2007).

As a synthesis of BAM thinking, and how it applies to the general challenges involved in ENM, Saupe et al. (2012) explored implications of different configurations of the M and A constraints. Specifically, they explored four configurations: one dominated by M, which they denoted "Wallace's Dream", and one dominated by A, which was termed "Hutchinson's Dream"; they also explored two extreme cases: one in which each constraint participates about equally in shaping the overall picture ("Classic BAM"), and one in which the two constraints coincide more or less in their constraining action ("All Fine"). The study showed that models for virtual species that were Wallace's Dream or All Fine configurations were rarely able to anticipate distributions of species better than random predictions – we note that those distributional situations are not at all rare, and yet many ENM studies have calibrated models for such species, and interpreted their implications, with unknown consequences (e.g. Gür 2013).

Where things start to get seriously complicated is in moving back and forth between G and E spaces. Note that, although N_F is one of the chief factors that determine G_O, we have no guarantee that all of N_F will be represented across G. That is to say, in formal terms, $N_F \cap \eta(G)$ will be smaller than N_F, such that not all of N_F is observable anywhere. What is more, if we consider that (by definition) the only areas that the species has "experienced" (i.e. reached by dispersal) is M, then a still-smaller set of conditions, $N_F \cap \eta(M)$ is the observable portion of the fundamental ecological niche; this set of conditions is termed the existing fundamental ecological niche, or N_F^*. Whereas N_F^* should suffice for identifying habitable areas across M, it will be limited in relevance and applicability for any environmental conditions of interest that are outside of $\eta(M)$. The realized niche, N_R, is the reduction of the existing fundamental niche by the geographic effects of species interactions, and is extremely complex to characterize (Chase & Leibold 2003).

The key point is that it is N_F that is the evolved suite of coarse-resolution translations of physiological parameters that make up the so-called Grinnellian ecological niche: without robust estimates of this quantity, many of the lofty goals of ENM will fail to be realized (Anderson 2012). These considerations are developed in greater detail and with more formality in Peterson et al. (2011), which indeed has even been criticized for entering into overmuch mathematical formality (Giles 2005). However, the formality allows some very useful insights, which we will explore in the remainder of this section. A good starting point is the following set of equations and inequalities:

$N_F \supseteq N_F \cap \eta(G) \supseteq N_F^*$ (reads: only a subset of the conditions associated with the fundamental ecological niche is necessarily represented across the surface of even the broadest regions on Earth).

$N_F^* = N_F \cap \eta(M) \supseteq N_R$ (reads: the existing fundamental niche is the reduction of the fundamental niche to the conditions accessible to the species).

$N_R = N_F^* \cap \eta(B) \supseteq \eta(G_+)$ (reads: the realized niche is the subset of the existing fundamental niche that is also suitable in terms of biotic conditions for the species).

$\eta(G_+) = N_R \cap \eta(S)$ (note: even N_R will be broader than the set of environments associated with the known occurrences of the species).

We hasten to note that our set-based notation is convenient, but perhaps does not account for the full complexity of some situations, such that kernel density functions may prove far more appropriate in complete solutions to some of these questions (Kramer-Schadt et al. 2013). Although we admit freely that our level of formalism is cumbersome, and certainly does not make for easy reading, we will return to these inequalities at several points in the remainder of this review. Use of this formal expression should make key implications much more clear than would otherwise be possible.

M *limits what is observable*

This point is clear and obvious on one level (i.e. we do not know how lowland gorillas would respond to Arctic temperatures or conditions on Mercury), but insidious and subtle on others. That is, the area to which the species has had access over its history may be an island or an interfluvium, delimited by factors having no environmental manifestation other than impeding dispersal. Within M, we can make the reasonable assumption that unoccupied sets of conditions are not inhabited because the conditions are not appropriate for the species; however, conditions not represented within M have by definition not been experienced by the species, such that the species' response to those conditions will remain at the level of guesswork. The

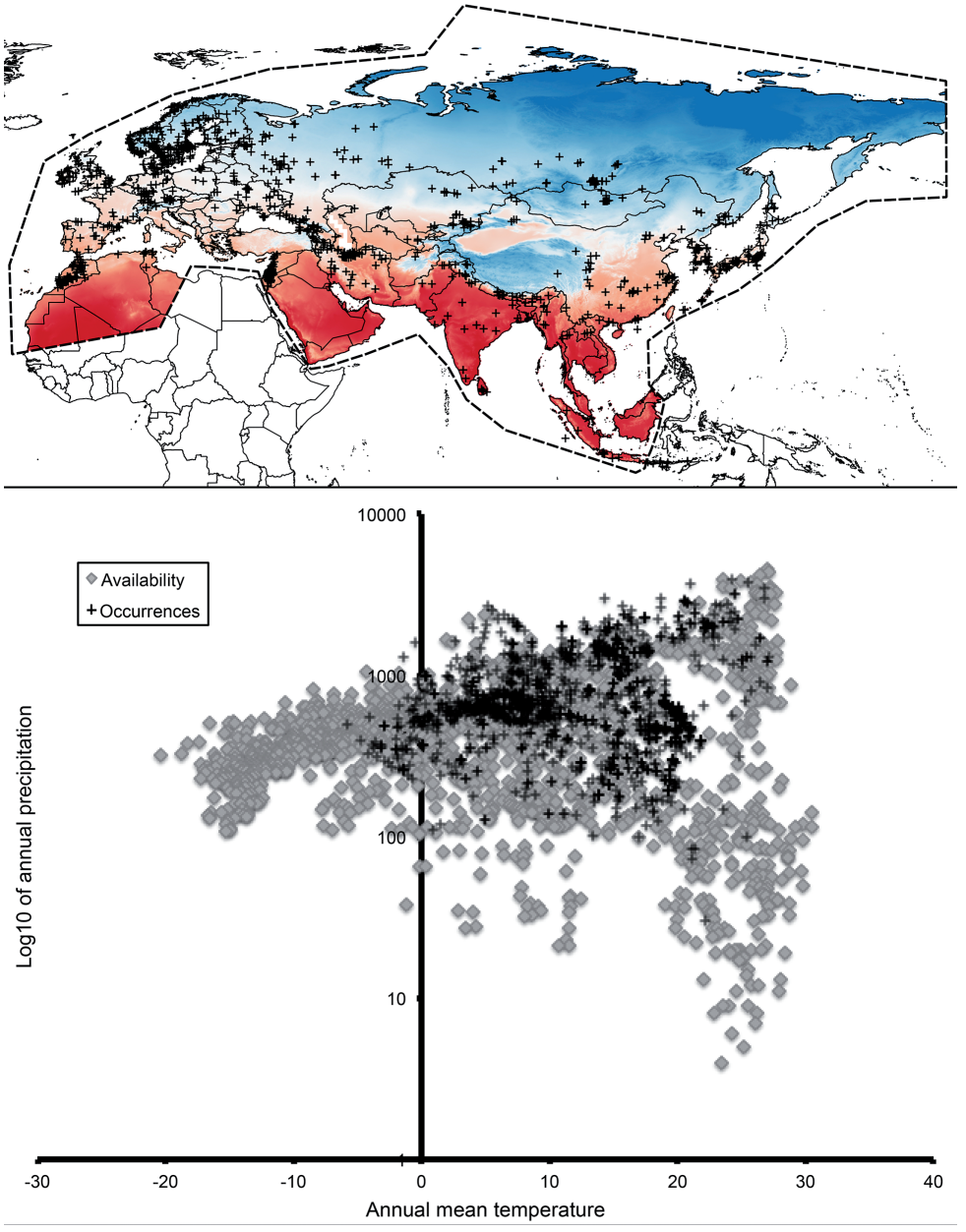


Fig. 1. View of the distribution of the great tit (*Parus major*) in geographic and environmental dimensions. Top panel: dashed line indicates a hypothesis of M, which conservatively excludes parts of North Africa that are not clearly within the dispersal potential of the species; black crosses (+) indicate known occurrences; and the shading summarizes variation in annual mean temperature (WorldClim data, 10' spatial resolution). Bottom panel: plot of known occurrences (+) in a space summarizing annual mean temperature and annual precipitation (note $\log_{10}$ scale); gray diamonds indicate conditions present across the M hypothesis, based on 3000 random points cast across the region.

implications of different assumptions regarding M, or even of ignoring M considerations entirely, for model calibration, model evaluation, and model comparison in ENM applications, have been examined in detail by Barve et al. (2011) and Anderson & Raza (2010). Beside methodological considerations, however, the effects of M are even deeper in ENM applications. That is, consider the range of the great tit across Eurasia (Fig. 1): this species would fall into the Classic BAM scenario, as the species' distribution is confined to Eurasia, not reaching Subsaharan Africa, America, or any oceanic islands, and yet large portions of Eurasia contiguous with the species' range are unoccupied, suggesting effects of A. Note in particular the distribution of the species with respect to the availability of conditions across M: although annual mean temperatures much below 0 °C clearly appear inimical to this species, the response to low precipitation and higher temperatures is more diffuse and less clear-cut. Most dramatically, however, note that the species' response to higher levels of precipitation remains completely uncertain – the species is found up

to the highest levels of precipitation that are available across its M, and no limit (i.e. accessible sites not inhabited) is discernable. What would this species do were it to encounter higher-precipitation sites? Quite simply, this information does not exist for this species, and any extrapolation into those conditions will be just that: extrapolation beyond the conditions for which any data were available.

Model transfers are dubious

In some sense, any attempt to classify landscapes that were not explicitly sampled as suitable or unsuitable is a model transfer and will include some level of uncertainty. However, a minor interpolation across a few pixels is less extreme than a transfer across a broad, unsampled region; model transfers among major regions and continents may be still more risky because aspects of the biotic environment may also differ in tandem with the environmental variation (Peterson 2003). Finally, most relevant to this contribution, projections to other time periods may be still more risky, as not only can the biotic component differ, but also even the correlation structure of the environments may differ as well, making those transfers particularly sensitive.

This latter situation should be explored in greater detail. That is, a typical phylogeographic ENM application will wish to hypothesize and test possible refugial areas in the Pleistocene for the species under study – clearly, such information would be useful in the case of the great tit example that is the focal example in this paper. Occurrence-environment correlations (= niche) are estimated from associations under present-day conditions, and then transferred to paleoclimatic scenarios, generally derived from general circulation model outputs. Owens et al. (2013) explored the consequences of such transfers when environments across M are not representative of those across the broader area of interest, i.e. $\eta(M) \subset \eta(G)$ and found massive and biologically unrealistic model projections that were, to be honest, in no way justifiable or reliable as a basis for scientific explorations.

Although the paleo-projection paradigm has seen criticism recently (Davis et al. 2014), the critique was not without its own problems. That is, the Davis et al. (2014) analysis took 7-year-old niche models published previously by Waltari et al. (2007), and "tested" them using paleo-occurrence data from fossil sites, but over a distinct time period, such that the test was rather makeshift. What is more, the models being tested were based on methodologies and data streams that were seven years out of date in a fast-evolving field: quite simply, the "test" that was erected was not particularly rigorous.

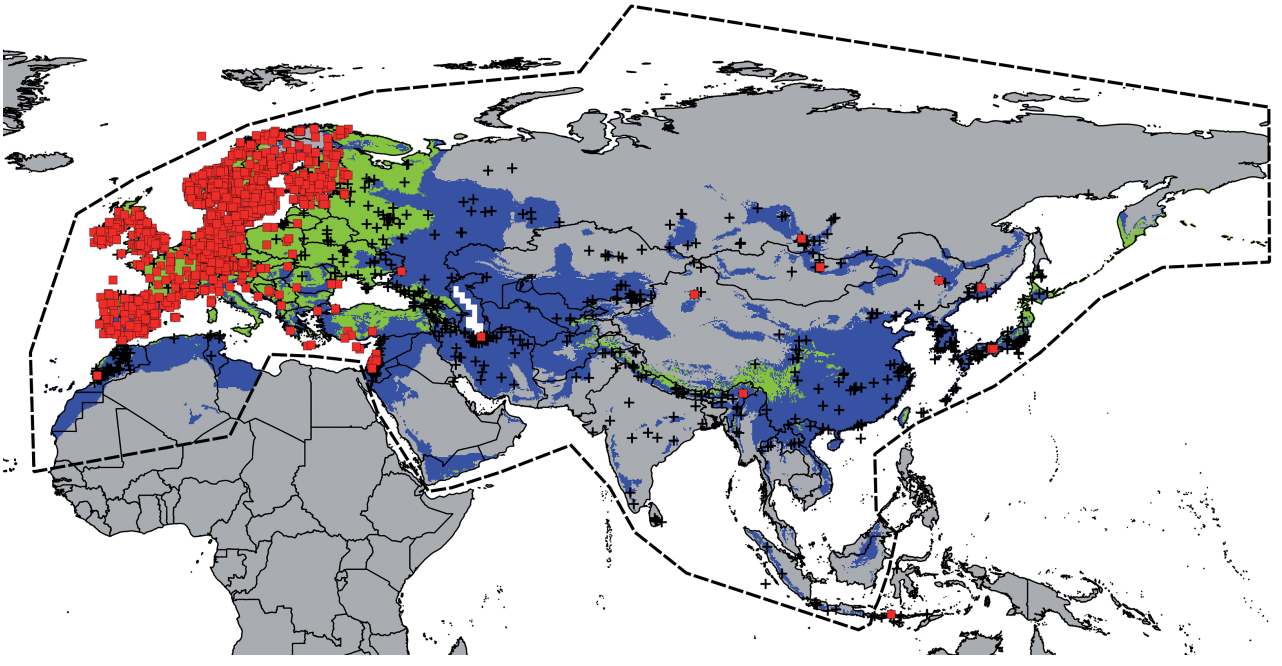


Fig. 2. Illustration of the known present-day geographic distribution of the great tit (*Parus major*) across Eurasia. The dashed line summarizes a hypothesis of M for the species. The red points (concentrated in Western Europe, but with a few scattered representatives across Asia as well are a random sample drawn from the 1.5M occurrences available for the species; the black crosses (not visible in Western Europe) represent a distinct sampling that strove to balance representation of different regions within Eurasia in the occurrence data set. Areas shaded in green are those deemed suitable by a model based on the random sample (red points); areas shaded blue were determined suitable by models based on the more spatially balanced occurrence data set (black crosses).

And more

This summary will necessarily remain a bit incomplete, as many decisions and uncertainties remain to be resolved and assessed. That is, myriad details must be explored and assessed in rigorous ENM applications: which sources of occurrence data can and should be used in ENMs (Lash et al. 2012), how to deal with uneven sampling across complex landscapes (see illustrations of this point in next paragraph), which of the many algorithms available should be used for model calibration (Elith et al. 2006), which sets of parameters should be used for a given algorithm (Warren & Seifert 2011), how to set thresholds for distinguishing between suitable and unsuitable predictions in model outputs (Liu et al. 2013), and how to evaluate niche model predictions rigorously (Peterson et al. 2008), among many other complexities. Much more detail has been offered about these considerations in two recent book-length treatments of ENM approaches (Peterson et al. 2011, Peterson 2014).

As an illustration of the fact that these methodological considerations are not trivial, we will return to the great tit example. The species' range covers a massive area, extending from Great Britain and the Iberian Peninsula across all of Eurasia to Japan and Indonesia; clearly, the density of birdwatchers is greater at the western extreme of the species' distribution than across Eastern Europe or Asia, as can be appreciated from Fig. 2. If not controlled, these sampling biases (and indeed more subtle ones as well) translate into biases in the models that result from ENMs; these effects can be seen in the minimal areas in Asia identified by ENMs when raw, unbalanced data were used in model calibration (Fig. 2). Although the point may seem obvious, and has been made under much more detailed and controlled circumstances in other publications (Peterson et al. 2014), many modeling efforts using ENM make no effort to control for such biases (e.g. Fichet-Calvet & Rogers 2009, Pigott et al. 2014).

Niche model outputs

Researchers use ENMs in phylogeographic studies to obtain – generally speaking – four sorts of results. These uses to which ENM techniques are put range from extremely simple to quite complex. Clearly, the opportunity for methodological gaffs and mis- or over-interpretations increases with the complexity of the application.

Distributional potential

At the very simplest, ENMs provide a useful perspective on the distributional potential of species. That is, in situations in which the species of interest is poorly known or poorly documented, ENMs can offer testable hypotheses as to its full distributional potential. Such hypotheses can guide sampling, and also can assist in interpretation of results: phylogeographic breaks in the midst of continuous potential distributional areas are far more interesting than those that coincide with distributional disjunctions (Tocchio et al. 2014).

Niche conservatism

One of the earliest explorations of niche focused on phylogenetic conservatism of ecological niches over the periods of evolutionary history that separated sister species pairs of birds, mammals, and butterflies in southern Mexico (Peterson et al. 1999, Warren et al. 2008). These results reflected interestingly on the evolutionary processes that produce biological diversity, but also provide the basis for model transfers: if niches evolve easily, and change frequently and/or unpredictably, then model transfers based on niche estimates in the present day are unlikely to be informative about past distributional potential.

Simple refugium hypotheses

A further level of inquiry in phylogeographic applications of ENMs is in positing spatially explicit hypotheses of refugia for species. That is, if climatic changes drive range disjunctions that create opportunities for population differentiation, generally over the Pleistocene (Haffer 1969, 1974, Simpson & Haffer 1978), and if fundamental ecological niches are conservative over evolutionary time periods (Peterson et al. 1999, Peterson 2011), then paleo-transfers of ENMs offer the opportunity to reconstruct the geography of suitable areas (G_p) at key points in the past. Such refugium-oriented analyses have been perhaps the most common application of ENMs in phylogeography, with numerous examples available (Hugall et al. 2002, Peterson et al. 2004, Ruegg et al. 2006, Peterson & Nyári 2007).

Assumptions regarding ways in which species have responded distributionally to climate changes are not as general as has generally been assumed (see detailed example in Gür 2013). Even among species inhabiting a single climate zone, modeled responses to Pleistocene climate changes have proven to be rather individualistic (Gür 2013). More detailed studies will have to be carried out, such that the generality of the glacial-refugium paradigm can be assessed. Indeed, Perktaş et al. (2015), studying phylogeography and paleodistributional potential of an Asian nuthatch species, concluded that the usual model does not

appear to hold true; rather, they found considerable complexity as regards the distribution of the species, particularly in interglacial periods.

Diversification scenarios and predictive biogeography

As experience builds with ENM applications to historical questions, and as relevant evidence accumulates, applications can progress from simple hypotheses of refugial geometry to more complex scenarios of diversification. For example, South America presents a fascinating mosaic of vegetation types and biomes that are adjacent, but that have contrasting historical patterns, as can be appreciated from ENM paleoprojections of elements from the Amazon Basin, the *cerrado*, and the montane habitats of the Andes (Bonaccorso et al. 2006, Peterson & Nyári 2007, Bonatelli et al. 2014). These contrasts translate into differing expectations regarding the timing of speciation events and ages of lineages in these different biomes (Peterson & Ammann 2013).

These rather descriptive approaches can also transform into predictive viewpoints as well. An emerging body of work (Carnaval & Moritz 2008, Davis et al. 2014) explored the predictive ability of measures of climatic stability across the Atlantic forest biome of eastern Brazil as regards the spatial distribution of genetic diversity and species-level diversity. In effect, these authors transformed hypotheses of climate-driven population stability into testable hypotheses of biological diversification, which is a more powerful inferential approach to difficult and complex questions in science. That is to say, used properly, ENM tools can provide exciting and testable hypotheses for phylogeography about where distinct lineages may be found, and about the timing of key historical events.

Pitfalls

Very simply, ENMs are an evolving technique, particularly when model transfers across broad distances in time and space are involved. Until recently, no field-wide synthesis had been offered, either conceptually or empirically (Peterson et al. 2011), and certainly no methodological stability or consensus has yet been reached. Most commonly, mistakes that are made are those of overinterpretation of the evidence that actually exists.

An excellent example of overinterpretation is that of conclusions regarding niche differentiation among populations or species. Very commonly, phylogenetic studies of niche evolution have been based on N_F^* estimates derived from ENMs, without regard to which parts of N_F are actually represented across M, which can lead to wild extrapolation of niche limits (Owens et al. 2013), and such methodological gaffs lead to inappropriate tendencies to conclude niche differentiation (e.g. Medley 2010). Indeed, a growing tendency is to estimate niche dimensions as $\eta(G_+)$, which is maximally limited and constrained by factors unrelated to N_F.

In either case, it is easy to envision a situation in which N_F is completely stable and conserved, and yet N_F^* varies considerably as a function of variation in $\eta(M)$, and similarly if $\eta(G_+)$ were used. That is, vicariant speciation is considered the dominant mode of speciation (Coyne & Price 2000), which will place closely related species in different areas, at least initially. These different distributional areas are structured by barriers to dispersal, such that each descendent species will have a distinct M, and by extension $\eta(M)$. This place-based (rather than niche-based) variation in sets of environments will introduce significant variation into N_F^*, $\eta(G_+)$, or any other measure of niche that is not N_F (Soberón & Peterson 2011). Recent papers that have fallen into this trap of overinterpretation (Kozak & Wiens 2010, Wiens et al. 2013) have simply not addressed the important methodological considerations that shape their biological interpretations; the field of invasive species biology is similarly rife with such overinterpretations (Peterson 2011).

Another pitfall in ENM applications to phylogeography is that of confusions of scale and resolution. Numerous methodological points can reduce the resolution with which geographic phenomena can be discerned in such analyses: sources of occurrence data, precision with which occurrence data are described, uncertainty associated with occurrence data, and the precision and resolution of the environmental data employed. Each of these considerations coarsens the real resolution with which it is possible to discern phenomena of potential interest.

For example, many researchers have fallen into the temptation to derive occurrence data for ENM analyses by plotting random points within polygons representing summaries of biological distributions; for example, a recent analysis of distributions of seasonally dry tropical forests in South America failed to find evidence of expansion of these habitats under glacial maximum conditions (Werneck et al. 2011); while such may indeed be the case (it is a matter of debate), the coarse and uncertain nature of the occurrence data used in that analysis represent a serious limitation and impediment to interpretation of their results. Similarly, a recent study argued that Central

American tropical forest trees had not "retreated" to climate-driven refugia under glacial maximum conditions (Poelchau & Hamrick 2013): again, although the result may be correct, methodological considerations enter the picture rather significantly. The native spatial resolution of the general circulation model outputs on which those analyses was 2.8° (i.e. on the order of 300 km), resampled to 2.5′ resolution (about 4 km) via bilinear interpolation – the Central American Isthmus is 65-250 km wide, such that many crucial climate parameters were surely obscured thanks to this seemingly innocuous methodological feature. Throughout, the point is that interesting biological points can get lost when uninteresting methodological considerations can produce the same, or similar, effects (Peterson & Nakazawa 2008).

A final, and perhaps crucial, example of methodological gaffs in ENMs relevant to phylogeographic applications is that of mistuned and overinterpreted model transfers. As discussed above, model transfers that go beyond simple and minor interpolation are perilous. In effect, when unknown sectors exist in the characterization of a species' response to a given environmental dimension (as in responses to higher precipitation in Fig. 1), no evidence exists that can guide fitting a response in a model: rather, we depend on how each algorithm extrapolates. For example, MaxEnt's default setting is to use "clamping" as a means of extending peripheral model suitabilities to more extreme values: clamping simply fixes the suitability value at the extreme of the calibration range of environments as the value for all more-extreme values (Owens et al. 2013). Under such assumptions, if a species is prospering in warmer parts of, say, Great Britain, then it would also be perfectly happy in the heart of the Amazon Basin, or at 200 °C, neither of which is a particularly satisfying conclusion. Owens et al. (2013) explored implications of these steps for conclusions of niche conservatism.

What could be

Phylogeography as a field has already achieved quite a bit: a synthetic and integrative body of theory and methods for understanding the behavior of genes and biological lineages over space. As discussed above, however, what is missing is explicit consideration of and hypotheses based on real-world landscapes underlying the molecular and phylogenetic patterns. A closer marriage of phylogeographic approaches with ecological niche modeling approaches thus has much to offer in enriching the field, and moving it towards a predictive, hypothesis-driven endeavor.

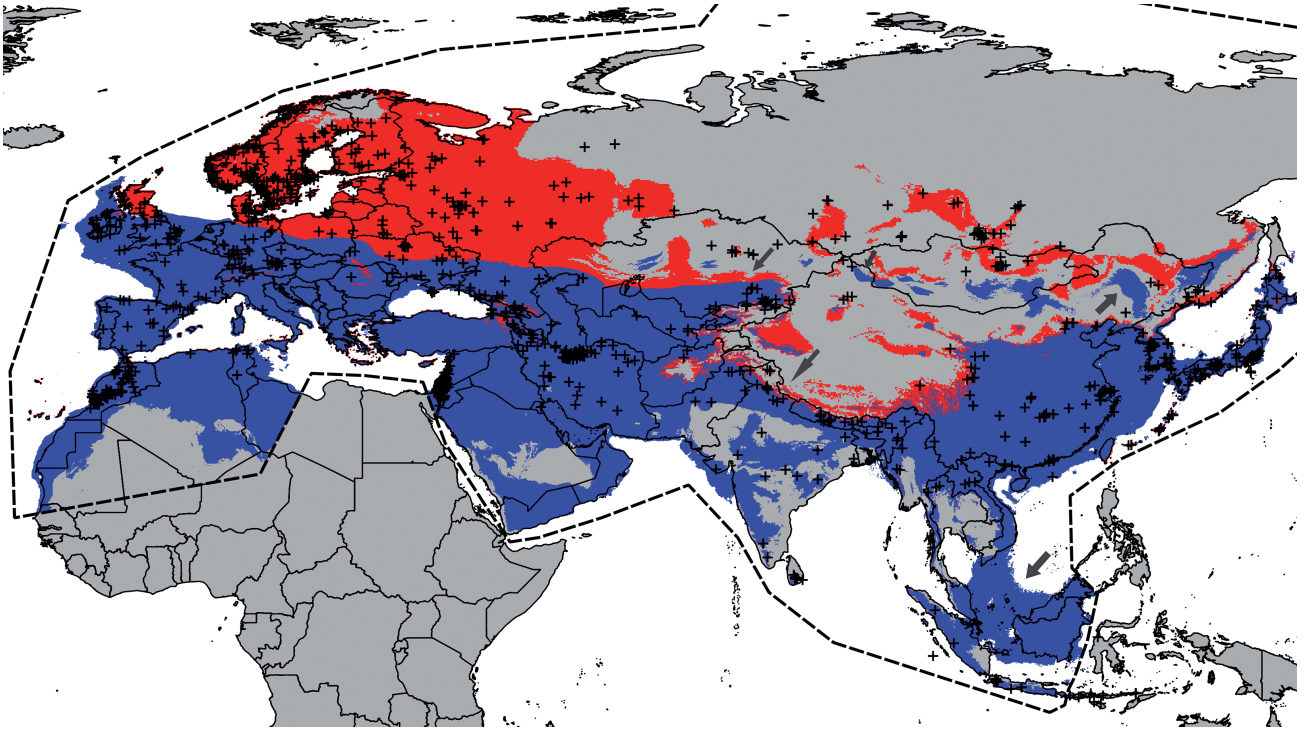


Fig. 3. Present-day and Last Glacial Maximum projections of ecological niche models for great tits (*Parus major sensu lato*) across Eurasia and North Africa. Dashed black line indicates the limits of the hypothesis of M used in model calibration. Black crosses indicate known occurrences of the species under present-day conditions. Red area shows present-day potential distribution (note that this area is partly obscured by the blue areas); blue area shows model transfer to Last Glacial Maximum conditions, as summarized by the MIROC general circulation model simulation. Arrows represent points of reference for discussion in text.

Consider the example to which we have referred several times so far in this contribution, great tits across Eurasia; Fig. 3 presents very preliminary and cursory paleoprojections (to the Last Glacial Maximum) of niche models for this complex of species (but based on occurrence data that have been rarefied to balance sampling spatially, unlike the example in Fig. 2). This complex has already been the subject of two phylogeographic analyses (Kvist et al. 2003, Zhao et al. 2012), such that we cannot be "predictive" in this example (i.e. we already know at least the general answers!), but the example can be useful and illustrative, and can even suggest some further analyses and tests.

The present-day potential distribution of this species extends broadly across Eurasia (Fig. 3), although less continuously in Central Asia. During the Last Glacial Maximum, however, the potential distribution of the species became still more bipolar, with major potential distributional areas in Europe and in East Asia (Fig. 3), connected only by a narrow string of areas along the Himalayas. This paleodistributional view offers some interesting thoughts that could be profitably explored further. (1) The potential distributional areas for the species in Morocco have been disjunct from European potential distributional areas for at least the last glacial cycle, and yet these populations do not appear to be strikingly distinct; perhaps a testable hypothesis that emerges is that this suite of populations then represents the result of a relatively recent colonization event. (2) Of the four candidate species taxa that phylogeographic studies have identified within the great tit complex, the European and north Asian *major* and the Central Asian *bokharensis* likely made up the western *major* distributional area for this complex in the Pleistocene. The isolation that produced the eastern form, however, could come from at least three sources (see black arrows in Fig. 3): *bokharensis* could represent the product of isolation in (1) small refugial pockets around minor mountain ranges in Central Asia, (2) the peninsula-like eastern limit of apparently continuous distributional areas that are broader and more continuous to the west, or (3) the narrow Himalayan potential distributional areas. Similarly, the isolation necessary to allow differentiation of the East Asian *minor* and *cinereus* could have been provided by northern population restriction to small refugial patches in northeastern China (orange arrow in Fig. 3), or in a more broad-ranging Sundaland area that is now mostly under water (purple arrow in Fig. 3). With sufficient sampling, testing among these explanations should be possible, providing independent corroboration of hypotheses between the geographic and molecular realms (Peterson 2009).

In sum, the possibility explored in this contribution is that phylogeography would become more than just phylogenetics of weakly differentiated populations across space. Rather, a truly synthetic phylogeography would complement molecular-genetic approaches and inferences with real-world views of distributional potential across complex, real-world geography. In addition, phylogeography would take into account the dynamics of the dramatic temporal variation that has occurred on the face of the Earth over the relatively recent past: the Pleistocene was a time of amazing dynamism that changed conditions radically, and moved species' potential distributions around rather dramatically. Complementing current distributions and current environments with information on past conditions would be an additional powerful addition to the phylogeographic toolkit. Phylogeography thus has real potential to become more predictive and less explanatory, arriving at tested hypotheses of biological diversification and biogeographic processes.

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