Mechanistic and Correlative Models of Ecological Niches

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ABSTRACT

The suite of factors that drives where and under what conditions a species occurs has become the focus of intense research interest. Three general categories of methods have emerged by which researchers address questions in this area: mechanistic models of species' requirements in terms of environmental conditions that are based on first principles of biophysics and physiology, correlational models based on environmental associations derived from analyses of geographic occurrences of species, and process-based simulations that estimate occupied distributional areas and associated environments from assumptions about niche dimensions and dispersal abilities. We review strengths and weaknesses of these sets of approaches, and identify significant advantages and disadvantages of each. Rather than identifying one or the other as 'better,' we suggest that researchers take great care to use the method best-suited to each specific research question, and be conscious of the weaknesses of any method, such that inappropriate interpretations are avoided.

1. NICHES AND DISTRIBUTIONS

The many and diverse concepts associated with the term 'niche' have long been central in ecological thinking (Chase & Leibold 2003). After a period of stagnation (approximately 1980-1990), during which research about niches was minimal (McInerny & Etienne 2012a, b), the term has seen a vibrant rebirth in recent decades. This revival appears associated at least in part with the possibility of using large databases of primary biodiversity occurrence data in tandem with geospatial data sets summarising environmental variables to estimate coarse-grained aspects of species' niche dimensions. By extension, from such niche estimates, one can then estimate potential distributional areas of species as well (Peterson et al. 2011).

This approach is the so-called 'correlative' approach to what has been termed ecological niche modelling (hereafter 'ENM'), in situations in which focus is on understanding conditions that allow persistence of species' populations, or species distribution modelling ('SDM') in situations in which focus is on predicting the geographic distribution of the species (Peterson & Soberón 2012). Other approaches to these challenges exist as well, however, such as 'mechanistic' niche modelling (Kearney & Porter 2009), that aims to understand, using detailed biophysical modelling approaches, the environmental requirements that make up the fundamental niche of a species; and 'process-oriented' or 'hybrid' distribution modelling (Dormann et al. 2012), wherein hypotheses about niche, dispersal, and (in some cases) biotic interactions are integrated in models and simulations of the entire set of processes leading to the occupation of areas by a species.

Some authors prefer to blur distinctions between these approaches (Dormann et al. 2012), and clearly the three do overlap and interlink (e.g., correlational or mechanistic niche estimates being used in process-oriented approaches). How-ever, here, we posit that the distinctions between mechanistic, correlative, and process-oriented approaches are more than just technical or methodological in nature, but rather that they correspond at least roughly to distinctions between three types of niches that are being estimated. This distinction

is crucial to the progress and advancement of detailed understanding of the distribution and ecology of species. This paper thus sets out to review these three approaches that are often perceived as competing (Kearney 2006) or as a part of a continuum (Dormann et al. 2012).

1.1. Background

The popularity of correlative ENM and SDM approaches in ecology and biogeography can be understood as elaborations by recent research groups on concepts presented originally by Grinnell (1914, 1917, 1924) and Hutchinson (1957). Key ideas include (1) the supposition that the geographic distribution ('range') of a species relates closely to its physiological and behavioural features (from Grinnell 1917). This point was later elaborated by Hutchinson (1957, 1978), in his idea of a 'biotope', defined as the geographic area across which the niche requirements of a species are fulfilled. (2) The niche can be represented as a multidimensional object enclosing the set of environmental conditions that a species requires for reproduction and survival (Hutchinson 1957). (3) At least three types of niches can be recognised: the fundamental (requirements only) and realised (modification of the fundamental to include effects of biotic interactions) niches, as well as an intermediate entity that later authors termed the 'potential' (Jackson and Overpeck 2000) or 'existing' (Peterson et al. 2011) niche; Hutchinson hinted at this latter niche type, but only very briefly (Hutchinson 1957, 1978). The point is that, whereas the fundamental niche is defined in strictly environmental dimensions sans geography, the existing niche represents the subset of the fundamental niche conditions that is actually represented on real-world landscapes that are relevant to the species (Peterson et al. 2011). Although still other types of niches (e.g., the 'tolerance niche') can be recognised (Sax et al. 2013), we are working within a reductive framework that has been outlined in a recent book co-authored by two of us and colleagues (Peterson et al. 2011). Finally, (4) Hutchinson (1957, 1978) perceived that separating different types of environmental variables as they relate to ecological niches would open doors to important theoretical advances, which has clearly been the case.

Thanks to a few decades of progress in population biology and biogeography, the above points can be defined and explored more rigorously in terms of the population processes that underlie the so-called 'BAM' diagram (Figure 1), a heuristic for the joint effects of biotic, abiotic, and movement (dispersal) considerations. The fundamental niche is now conceived of as a scaled translation of the suite of physiological tolerances within which a species is able to maintain populations without immigration subsidy (Peterson et al. 2011). Whereas physiological tolerances are organismal responses to conditions on microscales (perhaps 10^{-3} m), most environmental dimensions that are used in ENM or SDM studies are much coarser, on the order of kilometres or more (10^3-10^4 m). This scaling of physiology into niche constitutes, in the end, one of the tougher challenges in building a rigorous conceptual underpinning of the broader endeavour of translating between organismal characteristics and geographic distributions (Barve et al. 2014).

On geographic extents, to a first approximation (i.e., ignoring high-resolution habitat preferences and the potential for evolutionary change in niches), regions of the world (hereafter termed **G**) exist where the physiological requirements of a species are fulfilled (hereafter **A**). Regions where the biotic milieu is suitable for the species are called **B** and regions that have been accessible by dispersal to the species over relevant time periods are called **M** (for mobility). The intersection of these three areas, termed the occupied distribution ($\mathbf{G}_O$), is the area in which viable populations of a species can potentially persist, and may be found. The counterparts of some of these geographic areas in environmental space are a set of reductions of the fundamental ecological niche ($\mathbf{N}_F$). These niche entities include the 'existing' fundamental niche (termed $\mathbf{N}_{F^*}$), which can be represented as $= \mathbf{N}_F \cap \eta(\mathbf{M})$ (where $\eta(\mathrm{X})$ can be interpreted as 'the environments associated with X'). The 'realised' ecological niche ($\mathbf{N}_R$) can be represented as $\mathbf{N}_F \cap \eta(\mathbf{M}) \cap \eta(\mathbf{B})$, and thus incorporates the effects of biotic interactions as well. These definitions are elaborated and explored further in Box 1.

1.2. Estimation

As mentioned previously, three major approaches exist within this broader field: mechanistic modelling, process-based modelling, and correlational modelling. Note that the latter subsumes both ENM and SDM, which have too often been confused or synonymised, an unfortunate practice that obscures important conceptual distinctions (Peterson & Soberón 2012). Curiously, and to a large degree the main point of this paper, these three approaches in reality estimate three different niche types such that debate among these approaches to a significant degree is a matter of comparing apples and oranges.

If one measures tolerance limits of a species with respect to a set of environmental dimensions via physiological experiments (Birch 1953; Kellermann et al. 2012; Barve et al. 2014) or first-principles biophysical models (Kearney & Porter 2009; Buckley et al. 2010; Higgins et al. 2012), one is measuring the multidimensional projection of a theoretical, fundamental niche onto a simpler space consisting of the set of variables that is actually being measured or modelled (Drake 2015). Such efforts are invariably carried out in relatively few environmental dimensions (e.g., temperature, water stress), as the complexity involved either in carrying out all of the factorial experiments (physiological measurements) or in estimating all of the relevant parameters (biophysical models) cannot be easily addressed. Although mechanistic niche models indeed estimate dimensions of the fundamental niche, translation of those estimates into potential geographic distributions requires significant assumptions about variation in many other dimensions. Scaling of parameter estimates and conditions across orders of magnitude of difference between physiological and geographic realms is a complex issue that has not been considered in detail.
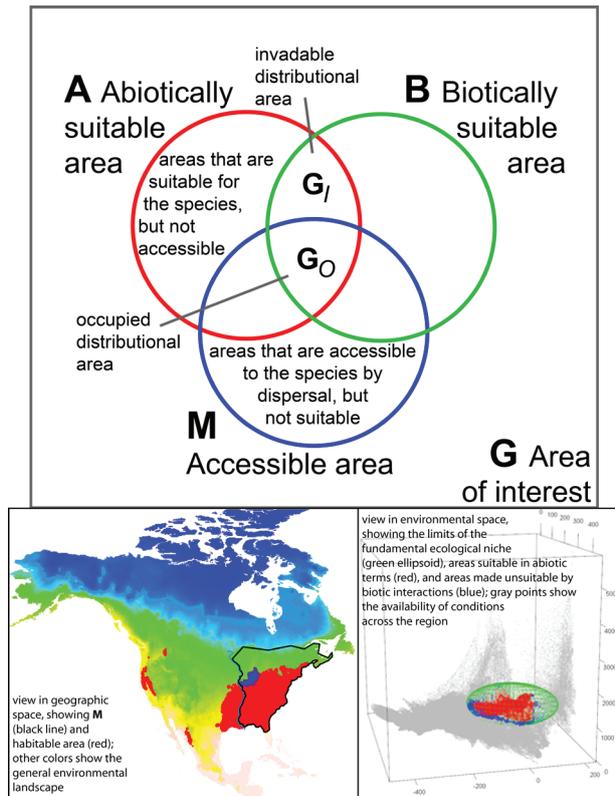
Figure 1. *The BAM heuristic for understanding the drivers of species' geographic distributions. Top: diagrammatic representation of effects of biotic, abiotic and mobility considerations; particular distributional areas are labelled and described. Bottom: linked views of the distribution of a hypothetical species in geographic (left) and environmental (right) dimensions. In geographic dimensions, the accessible area is shown as a black line (delimited by the Mississippi River to the west, Gulf of Mexico to the south, Atlantic Ocean to the east and distance to the north). The habitable areas (i.e., conditions within the fundamental ecological niche) are shown as red and dark blue (the remaining colours, including blue areas in the far north serve only to summarise general environmental variation). Note that portions of the habitable area are inside and other portions are outside the accessible area and some are broadly disjunct from the occupied area. The dark blue areas in the central United States indicate the presence of a competitor species that affects the distributional potential of the species. In environmental dimensions, the fundamental ecological niche is visible as the green ellipsoid and habitable sites on the landscape of North America are those coloured red or blue within that ellipsoid. The reductive effects of the presence of the competitor species can be seen as the blue edging around the fundamental ecological niche. Note also that major portions of the fundamental ecological niche are not represented anywhere within North America; the portion of the ellipsoid that indeed is represented within the Americas and more particularly within the species' **M**, is the existing fundamental ecological niche.*

Correlative methods (Guisan & Zimmermann 2000; Franklin 2010; Peterson et al. 2011) have a distinct suite of advantages and disadvantages. Here, data characterising sites where the species is known to occur are related to the environmental characteristics of those localities. Although numerous such correlative approaches exist (Elith et al. 2006), most compare environments associated with sites of known presence to those associated with sets of sites that do not (or are not known to) hold populations of the species. By this means, but under rather restrictive and too-often-ignored constraints (Anderson et al. 2003; Anderson & Raza 2010; Barve et al. 2011; Saupe et al. 2012; Owens et al. 2013), it is possible to identify sets of conditions under which the species is able to

maintain populations. These environmental correlates estimate a 'niche' that is almost certainly intermediate between the realised and the fundamental niches (Lobo et al. 2010), but its actual position is rather poorly defined - this point will be discussed further below.

Finally, several recent efforts have aimed to develop process-based models and simulations of the joint action of the suite of factors that together determine species' geographic distributions (Cabral & Schurr 2010; Dormann et al. 2012). These approaches generally require an initial hypothesis of the fundamental niche, hypotheses regarding dispersal ability across complex landscapes, a starting point, and (at times) hypotheses about interactions with other species. Process-based approaches ideally involve simulations such that the complexities of chance effects are also taken into account and appear in results as unusual possible outcomes. To the extent that these approaches are successful in approximating the full complexity of the situation, they create a detailed hypothesis of G_O that mirrors the geographic footprint of the realised niche (N_R).

1.3. This overview

This paper aims to provide a synthesis regarding approaches for estimating ecological niches and geographic distributions of species. We aim to derive a detailed understanding of the relative advantages and disadvantages of each approach, particularly in the face of real-world constraints of data availability, the biases that pervade such real-world analysis situations, and the data gaps that are similarly ubiquitous in this area of inquiry. Rather than a competitive situation in which one approach might be found to perform better overall than the others, the picture to which we arrive is one of complementary viewpoints. In particular, we note that many studies to date have used terminology and concepts cavalierly, creating considerable confusion of terminology and interpretation regarding similarities and differences among approaches. Indeed, appreciating the different niches that each approach approximates in reality, as the three approaches serve quite different purposes and will yield quite different answers, we would argue that any perceived competition among methodologies is mostly a consequence of misperception.

2. RELATIVE MERITS OF DIFFERENT APPROACHES

2.1. Mechanistic approaches

Mechanistic and biophysical approaches have the significant advantage of direct ties of quantities being estimated to the physiology of the species under consideration. As such, these methods have the potential for direct measurement of dimensions of the fundamental niche without the confounding effects of accessible areas and interacting species. In this sense, these approaches permit identification of the spatial footprint of **A**, without the complications related to **M** or **B** that certainly affect the other two approaches. When estimating future distributions under scenarios of climate change, for example, the

Box 1. Illustration of niches and distributions

The ideas in this box are based on the concept, from Hutchinson (1957), of a rather complex correspondence between niche space and geographic space, the so-called Hutchinson's Duality (Colwell & Rangel 2009). This idea is made operational by representing geographic space as grids with an extent and cell-size and environmental variables associated to each cell (Peterson et al. 2011), as in many raster GIS operations. Niches then are sets of points in the variable space at time t (which can be termed E_t); corresponding distributional areas are sets of coordinates in geographic space. The different types of niches (fundamental, existing, and realised) can be represented as subsets of the space E_t (note that in much of our discussion in this paper, we neglect the time-specific nature of these definitions). The symbols used in this discussion are modified slightly from Peterson et al. (2011).

Figure 1 depicts the biotic-abiotic-mobility (BAM) diagram as well as an example of linked environmental and geographic spaces, illustrating the complex topological connections between the two. The ellipse in the environmental space is a simple illustration of a possible fundamental niche N_F, but note that the entire ellipse is not observable under the suite of environmental conditions that is manifested on the ground. Rather, the set of habitable conditions that is the fundamental niche is intersected with the cloud of points in environmental space at a given time E_t, to identify points inside the ellipse. Reducing N_F further by intersection with the set of environments represented within the accessible area (**M**) for this species, we obtain a set of environments that is termed the existing niche, N_F^*, which is implicitly referred also to time t. The reduced nature of N_F^* with respect to N_F can be appreciated also in Figure 2.

Note that the geographic area corresponding to N_F^* in the examples in Figure 1 is broader than the occupied geographic distribution, including areas in western North America that are not inhabited by this species. Dispersal limitations that are subsumed in the concept of **M** make only temperate areas east of the Mississippi River accessible to the species, and hence within G_O. The remaining habitable areas are apparently outside of **M**, and as such, are termed the invadable geographic distribution (G_I): some are immediately west of the Mississippi River barrier, whereas others are broadly disjunct farther to the west.

Finally, since interactions with other species may further hinder full occupation of potential geographic distributions, the geographic and environmental footprint of even the existing niche may not be fully used by the species. This idea is expressed in Figure 1 as the geographic presence of a hypothetical competitor species (range shown in blue) and the reductive effects on its ecological niche that can be seen in the environmental-space visualisation. This further-reduced environmental potential is the realised niche (N_R); even this reduced niche nonetheless may still map onto both inhabited and uninhabited geographic areas as a result of finer-scale processes acting in parallel.

In the logic developed in this paper, then, the following relationships among niches should hold:

$$N_F \supseteq N_F^*, \; N_F^* = N_F \cap \eta(M_t)$$
$$N_F^* \supseteq N_R, \; N_R = N_F^* \cap \eta(B_t)$$

Note that N_R is the most restricted suite of environments, as it reflects the fundamental niche of the species in question, the environments represented across the accessible area for the species, and the environmental constraints placed on the species by other competing species. Almost all of these niches and sets of environments are time-specific: that is, they can and do change through time; the only exception would be N_F, which should change on much slower time scales, responding only to evolutionary change in the species' tolerances and physiological responses.
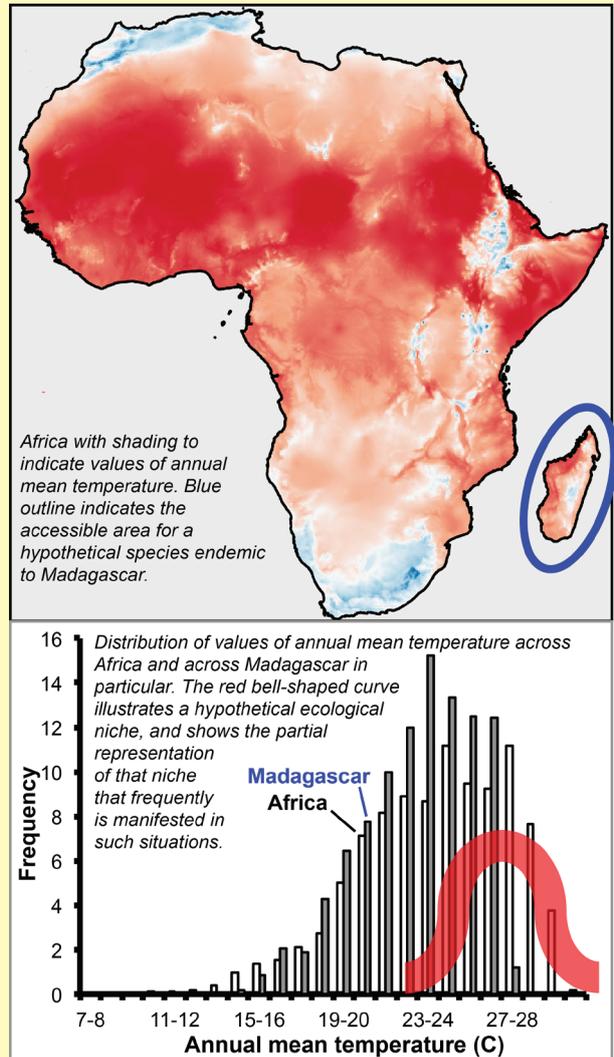

Africa with shading to indicate values of annual mean temperature. Blue outline indicates the accessible area for a hypothetical species endemic to Madagascar.

Distribution of values of annual mean temperature across Africa and across Madagascar in particular. The red bell-shaped curve illustrates a hypothetical ecological niche, and shows the partial representation of that niche that frequently is manifested in such situations.

Figure 2. *Illustration of the existing fundamental ecological niche for a hypothetical species endemic to Madagascar. The map (top) shows values of annual mean temperature across Africa. The 'species,' however, is endemic to Madagascar and thus, has a restricted accessible area* **M***, shown as the blue outline on the map. The environments represented across Africa and across* **M** *are contrasting, obviously, as can be appreciated from the histogram (bottom; white bars for Africa; gray bars for Madagascar). Note that a hypothetical ecological niche (see red bell-shaped curve on histogram) may not be represented completely across either* **G** *(here Africa) or* **M** *(here Madagascar). This reduced portion of the fundamental ecological niche that is observable is the existing ecological niche, and is what is observable in correlational ecological niche modelling studies.*

objective must be to measure the fundamental niche of the species, as that is the niche that determines the species' potential for response; thus, mechanistic modelling approaches may be more adequate for these types of investigations, although comparisons of future distributional estimates based on mechanistic and correlative approaches produced mixed results (Buckley et al. 2010; Kearney et al. 2010).

Mechanistic and biophysical approaches often assume that an estimate of the niche of a single individual or a few individuals will suffice to characterise the ecological niche constraints on the entire geographic range of the species in question. In many cases, this limitation is the result of practical considerations: physiological measurements and detailed parameter estimates needed for mechanistic model calibration are costly in terms of both time and resources. However, in light of considerable evidence of local adaptation in niche-related characteristics in many groups (Linhart & Grant 1996), one must also ponder the possibility that a single- or few-site characterisation of niche would underestimate the full ecological and environmental potential of such locally adapted species (Kearney & Porter 2009; note, however, that correlative models can be accused of the same failing as is detailed below). On the positive side, if detailed information exists to parameterise small-scale adaptation events, mechanistic modelling offers the possibility of fine-tuning niche estimates to reflect the specific niche characteristics of locally adapted individuals.

In addition, the reliability of physiological parameters depends on the source of this crucial information, whether gathered in natural settings or through laboratory experiments. The latter are potentially influenced by limitations specific to experimental situations such as acclimatisation, sample sizes, and length of life cycle (Lutterschmidt & Hutchison 1997; Simon et al. 2015). A further major constraint is in the scaling challenges mentioned above: mechanistic models and measurements are physiological in nature and as such represent individual characteristics that are relevant on extremely fine spatial scales, but are then applied to estimate geographic phenomena at coarse spatial and temporal scales. These constraints require assumptions, many of which influence the outcomes of the models (see Box 2).

Indeed, most mechanistic models tend to require large numbers of parameter estimates for model calibration and setup. For example, to estimate the microclimatic conditions, parameters related to soil properties, wind speed, solar radiation, and cloud cover are needed. However, such detailed information may not be available for many regions of the world, especially at fine spatial and temporal scales (Kearney & Porter 2009). Behavioural characteristics that affect heat, energy, and water fluxes (thermoregulation by seeking shade, burrowing, body posture changes, etc.) can also be difficult to parameterise at the spatial and temporal resolutions needed. Finally, measurements of body part dimensions, insulative properties of integument, and specific physiological parameters (e.g., thermal conductivity, oxygen extraction efficiency, diet, and digestive properties) may not be available for many

organisms; some of these parameters have been derived from allometric equations calibrated on better known model organisms (Kearney & Porter 2004; Natori & Porter 2007; Long et al. 2013). Estimates from single populations or based on allometric equations or measurements of other species may not be precise enough; Box 2 provides an illustration of the sensitivity of mechanistic modelling approaches to rather minor variations in parameter estimates. Errors in parameter estimations have been shown to affect mechanistic model performance (e.g., Buckley et al. 2010).

A further key consideration is how individual measurements are scaled up to landscape- or broad geographic-level predictions of organisms' energetic needs by applying the same energy balance equations. These extrapolations are calibrated in detail for one site, but are applied to all cells of a raster covering the geographic area of interest (Kearney & Porter 2009). An important complexity is that possible interactions among neighbouring cells that may affect the microclimatic conditions and organismal energetics are not estimated (Natori & Porter 2007).

Finally, the geographic area (**A**) identified by mechanistic models is of uncertain meaning. That is, if biotic interactions or dispersal limitation play significant roles in distributional ecology, then large portions of **A** may not be, in reality, habitable and reachable by the species (Wisz et al. 2013). Indeed, positive interactions may even open up additional distributional possibilities beyond the limits of **A** (Araújo & Rozenfeld 2014), as has been suggested for positive interactions among species in increasingly harsh environmental conditions (Bertness & Callaway 1994; Bruno et al. 2003), but that possibility is neglected in the reductive structure of the BAM diagram, which implicitly assumes that species interactions will be negative in nature. That is, even with a robust hypothesis of **A** in hand, the maps that result may not be particularly predictive or instructive; this limitation will frequently require that mechanistic approaches be linked with process-oriented approaches to be able to predict and anticipate distributional phenomena.

2.2. Correlative approaches

Correlative approaches have both advantages and disadvantages that are distinct from those of mechanistic approaches. Clearly, it is simultaneously an advantage and a disadvantage that correlative approaches measure something less than the full fundamental niche: as mentioned above, the meaning of estimates of **A** (the geographic footprint of the fundamental ecological niche) is unclear. That is, correlative model outputs express a complex combination of factors, including the effects of the frequently unknown **B** and **M**, whose combined restrictive effects (plus the effects of the sampling that underlies the occurrence data) shape species' distributions and constrain their estimation. The degree to which a view of **A** will include uninhabited areas is not known in many cases. On the other hand, the joint effects and interactions among abiotic, biotic, and dispersal effects can be rather complex: interpretation of

correlational models will always be compromised by this mixture, as joint effects will frequently not be able to be teased apart, distinguished, and interpreted completely and clearly (Soberón & Peterson 2005). Indeed, recent papers based on simulated species have demonstrated that some scenarios of joint effects of **A**, **B,** and **M** are impossible to disentangle and explore using correlational approaches (Saupe et al. 2012), particularly when models are to be transferred to other landscapes or times (Owens et al. 2013).

On the other hand, the advantages of correlational approaches centre on their low input data needs: because they require few predictor variables for calibration (although many parameter estimates may be generated in the process of model calibration), they are perhaps less dependent on availability of variables for the calibration process. What is more, because correlational models are keyed at the outset to geographic occurrences and coarse-resolution environmental dimensions, these approaches avoid the challenges of scaling up from individual phenomena to landscape-level phenomena. Their reliance on sampling of occurrences across the geographic distribution of the species provides a set of partial tests of niche tolerance limits: in this sense, correlational approaches avoid the single-niche assumptions of mechanistic models and can incorporate effects of numerous causal factors in a single 'model.'

However, correlative approaches have limited use in pinpointing fine-grain, individual-level tolerance limits. When local adaptation in niche-relevant dimensions has occurred, correlative models cast at the level of the species will overestimate the niche of any single population (whereas mechanistic models based on single populations will tend to underestimate niches in the same circumstances), and conversely niches estimated for single populations or subsets of species' overall distributions may underestimate the full breadth of the niche (Peterson & Holt 2003; Strubbe et al. 2015) or indeed fail to achieve a predictive model at all (Owens et al. 2013). Finally, very clearly, the vagaries of the sampling of biodiversity (e.g., spatial bias to accessible areas, incomplete sampling across an area, incomplete detectability of individuals) will have considerable potential to translate into new biases and problems in model outcomes (Hijmans 2012; Kramer-Schadt et al. 2013; Boria et al. 2014).

In sum, returning to the question of what is being estimated, 'niches' estimated by correlational approaches are complicated in terms of their interpretation. Correlational models will generally identify some suite of environmental conditions that fall in between fundamental and realised niches. Although, in that sense, they avoid the challenges of interpretation of the geographic footprint of **A**, they end up interpreting an uncertain mix of effects of **A**, **B,** and **M**. The geographic area identified by such models is neither **G**$_O$ nor the broader **G**$_P$ (the potential distributional area when dispersal constraints are relaxed), but rather something intermediate. Full interpretation of such models is complex and still requires additional assumptions and hypotheses to be able to interpret

model outputs clearly as distributional predictions (Peterson & Soberón 2012).

2.3. Process-oriented approaches

Numerous recent papers have attempted to estimate, model, or simulate components of the BAM diagram and their joint action in determining the geographic ranges of species (Rangel et al. 2007; Barve et al. 2011; Dormann et al. 2012; Lira-Noriega et al. 2013; Wisz et al. 2013). At the outset, each of these studies has had to find some means of approximating the fundamental niche, which has included simple assumption and postulation of niche size, position, and shape (Godsoe 2010); niches derived from mechanistic models (Kearney & Porter 2004); and niches estimated by correlational means (Schurr et al. 2012). That is to say, studies using process-oriented approaches in some sense must depend on and be built on prior niche estimates from the other two approaches. However, the end product of a process-oriented study is a hypothesis of **G**$_O$, which corresponds to a set of environments that in some sense approximates **N**$_F$.

The attractive aspect of process-oriented studies is that they are considerably more precise and explicit regarding what niches and distributions are being considered and estimated. Because they take dispersal into account directly and they pose specific hypothesis about the action of different factors in the BAM framework, process-oriented approaches may provide unique views into how access, dispersal, and colonisation act separately and jointly to drive many distributional details. Indeed, when simulations are developed, process-oriented models offer the unique possibility of testing and measuring the degree to which different factors do and do not affect particular species' niches and distributions.

Put another way, in the interest of making the discussion in this overview as explicit as possible, process-oriented studies are not concerned directly with *estimating* niches. Rather, they use estimates of niche dimensions and dispersal characteristics that, in turn, are used to simulate the processes that produce **G**$_O$. It is also possible to estimate parameters of such models using Bayesian approaches (Marion et al. 2012) that assume some prior distribution for the parameters of both niche and dispersal. Niche estimates in process-oriented studies should be of the fundamental niche, as the separate actions of dispersal limitation and interactions with other species are generally incorporated in the structure of the simulations and models. In translating fundamental niche estimates into realised niches and distributional areas, process-oriented studies contrast rather dramatically with mechanistic and correlational modelling approaches.

3. SYNTHESIS

3.1. Overview

This paper reviews three approaches that appear at least on the surface to estimate the same sorts of things: either the

ecological niche or the geographic distribution of a species. These approaches, however, respond to three rather distinct questions. In this sense, the different approaches do not compete; integrating two or more of these approaches can provide complementary information valuable in investigating the complexity of species' niches and distributions. Perhaps the continuum metaphor mentioned earlier is closest to what we propose; however, in view of the differences in objective, the question rather is under which circumstances each approach is most applicable or desirable.

Thus, the nature of the research question is key in determining which approach to use. At one end of the spectrum are what can be termed 'true' niche modelling challenges in which the goal is to estimate the geographic regions that are potentially favourable for a species, often at sites or under conditions that the species may not even have reached or yet be experiencing. Here, clearly, estimates of N_F are required, so physiological, biophysical, and maybe even behavioural information is needed. Mechanistic models may be most appropriate, at least in theory, as they provide direct estimates of N_F and thus of **A,** and those niches and distributional areas are those that approximate most closely the potential distribution, termed G_P in one recent synthesis; (Peterson et al. 2011). This appropriateness, of course, will depend on the degree to which such models can be parameterised adequately and sufficiently without undue reliance on general estimates or extrapolations. When such models are either not possible or not satisfactorily detailed and specific, correlational models may provide a second-best choice, but with careful consideration of the effects of **M** (Anderson & Raza 2010; Barve et al. 2011), BAM scenario (Saupe et al. 2012) and the need for extrapolation (Owens et al. 2013). That is to say, neither mechanistic nor correlational approaches provide ideal solutions to this challenge, but rather each must be used intelligently and in the context of its limitations.

At the other end of the spectrum, some studies have as a goal the precise and correct estimation of the actual geographic distribution of a species, such as in species-based conservation efforts. Here, clearly, 'just' a good estimate of the fundamental ecological niche (or the existing or realised niche) is not enough, as the correct conditions do not guarantee that the species will be present, although a first approximation is offered by a correlational model developed in the context of a carefully considered hypothesis about the limits of **M**. Any niche estimate will map onto broader geographic areas than the true G_O covers, such that niche estimates must be accompanied by hypotheses about the effects of dispersal and access, metapopulation dynamics, extinction, etc., if the model is to estimate G_O with any rigor and in any detail. This general modelling goal will thus fall most closely in line with what can be accomplished with process-oriented modelling approaches, either in a statistical sense (Dormann et al. 2012), or in a simulation environment (Barve et al. 2011). These approaches can, however, be quite computing- and data-intensive.

3.2. The popularity of correlational models

Correlative modelling has become extremely popular, since the idea was first explored in the 1980s and 1990s, with hundreds of papers appearing every year that use this general approach (Guisan et al. 2013). We believe that this popularity and rapid growth in interest and incorporation in diverse research avenues is in largest part owing to the massive growth in availability of biodiversity data and open-access analysis software. These data, which can be termed primary biodiversity occurrence data, have become massively openly and freely available via internet data portals such as the Global Biodiversity Information Facility, VertNet, eBird, speciesLink, REMIB, SABIF, Canadensis and many others (Thessen & Patterson 2011), such that on the order of more than 6.5×10^8 primary biodiversity records are now online and openly available. Data availability is mirrored by broad and accessible of tools for correlational ecological niche modelling: most (not quite all) of the major analysis platforms are either available for download and use freely (Maxent; Phillips et al. 2006) or are open-source, such as openModeller (de Souza Muñoz et al. 2011) or dismo (Hijmans et al. 2012) such that even the programming code can be downloaded and explored.

In spite of the massive (and growing) popularity of correlational modelling, this approach estimates a less-than-well-defined object, probably generally falling in between N_R and N_F^* (Lobo et al. 2010). To be able to understand and be confident that a particular correlative modelling exercise is yielding predictions that are useful for a particular study, considerable care and attention to detail are required, which suggests that many studies using this approach have not been sufficiently careful and lack analytical rigor (Araújo & Peterson 2012). To be able to interpret a correlational model correctly as in the challenge of approximating G_O *versus* G_P implied in the whole ENM/SDM debate (Peterson & Soberón 2012), ancillary hypotheses about movements and potential for movement (**M** in the BAM diagram) are required (Barve et al. 2011). Ideally, also, hypotheses would be available regarding presence or absence of any strong interactor species that might be involved (Bullock et al. 2000; Leathwick & Austin 2001). We note, nonetheless, that these same additional hypotheses are needed to be able to interpret the results of mechanistic models as anything other than the rather oddly defined area **A** (i.e., the area of potential distribution, regardless of access and in absence of biotic constraints).

3.3. Why not just mechanistic models?

In a recent overview of correlational models (Peterson et al. 2011), two of us (with other colleagues) stated considerable admiration of mechanistic modelling approaches based on the fact that they estimate dimensions of the fundamental niche directly. While we still adhere to that general statement in principle, in light of substantial further thought and experimentation, we are now perhaps a bit more guarded in our enthusiasm.

Box 2. Mechanistic modelling example: effects of parameter values on heat-energy balance calculations

Mechanistic modelling, as proposed by Warren Porter and colleagues (Porter et al. 1994), aims to calculate heat fluxes between an organism and its environment, and quantify the organism's metabolic processes (e.g., energy needs, water loss through evaporation). If energy, water, and nutrient needs can be determined in detail, it would be possible to predict growth and survival (Porter et al. 2010). Compared with correlative models, which do not establish linkages between organismal physiological processes and climate, mechanistic models are able to connect physiological function to climate (Kearney et al. 2014a). Such direct links can be established with respect to microclimatic conditions with which the organism actually comes in direct contact to estimate the organism's energy and water budget.

To calculate heat fluxes between the organism and the surrounding microclimate, information about its morphology, physiology, and behaviour is also needed. As a consequence, mechanistic models tend to require large numbers of parameters for model calibration (Kearney & Porter 2009; Porter et al. 2010). Mechanistic modelling ideas have been implemented in the program Niche Mapper™, which includes two components (see Figure 3): the microclimate model (i.e., the translation from macroclimate to microclimate) and biophysical model (i.e., the organism's interface with its surrounding microclimate) (Porter and Mitchell 2006). Hourly microclimatic conditions at the height of the organism are estimated from environmental variables (e.g., air temperature, humidity, wind speed, solar radiation) and are used in the biophysical model, along with the organism's allometric, behavioural, and physiological characteristics. Recent efforts to create global-extent microclimate datasets at 5 km spatial resolution (Kearney et al. 2014a; Kearney et al. 2014b) address one of the crucial data requirements of mechanistic models. However, the lack of detailed knowledge of species' morphology, behaviour, and physiology remains a significant barrier to use of mechanistic models in estimating species' niches. In applications of these approaches to date, as many as 60 parameter values have had to be specified, yet sensitivity of these methods to these has not been assessed rigorously.

Here, for illustration purposes, we explored the effects of minor modifications to 2 of the 13 physiological parameters from a published dataset for elk (*Cervus elaphus*) (Long et al. 2013). We created an artificial landscape of 5 x 5 cells, with a north-to-south gradient of air maximum temperature and an east-to-west gradient of relative humidity (Figure 4), keeping wind speed and cloud cover constant; we integrated these data in the NicheMapper™ microclimate model. We ran three biophysical models, one with the original published parameter values (Long et al. 2013), one in which we increased the maximum core temperature of the organism from 40.0 to 40.2°C, and one in which we increased the percent of energy released as heat that affects body core temperature from 80 to 81%. The result of these simple explorations of parameter value variation was that estimates of total evaporative water loss for the elk differed spatially, even with seemingly trivial differences in single parameters (Figure 4).
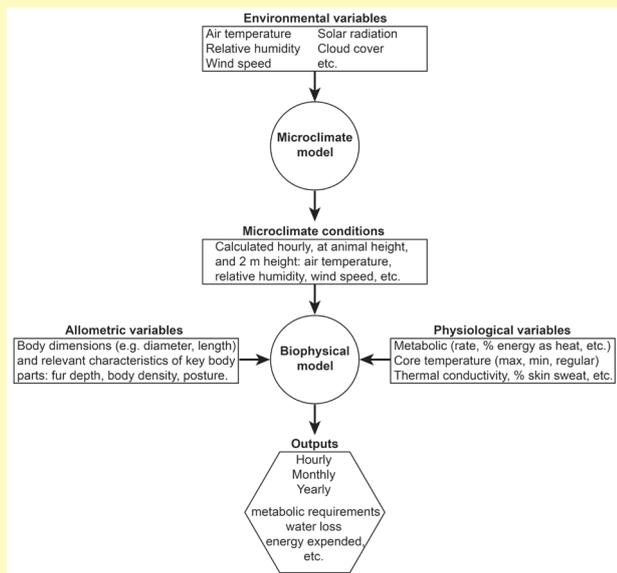

Figure 3. *Summary of information flow and data inputs to the mechanistic model. The effects of small perturbations and variations in parameter values on mechanistic models are illustrated in Box 2.*
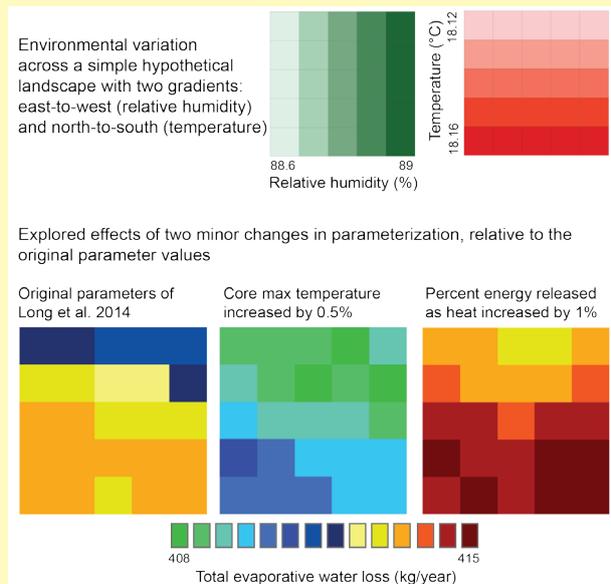

*Figure 4. Summary of explorations of variation of mechanistic models, using as starting point the Long et al. (2013) study of elk (*Cervus elaphus*) energetics. Our inquiry was based on a simple, hypothetical 5 x 5 pixel environmental landscape in which relative humidity and temperature vary independently (top). We changed values of two physiological parameters (out of many that are required for model development): effects on the evaporative water loss landscape for the species are shown in the panels at the bottom of the figure.*

Quite simply, we are increasingly aware of the 'estimation burden' that mechanistic models must bear. That is, few species out of the global sum of biological diversity have been the subject of detailed physiological measurements and even fewer have been the subject of first-principles-based mechanistic models. Indeed, the number of species that have been the focus of such fundamental niche estimation exercises is so small that new efforts must often rely on related species (or even rather unrelated species) for parameter estimates; Box 2 illustrates the implications of these assumptions. Also the numbers of parameters on which these models depend are generally quite large, in many cases numbering in dozens, such that overparameterization is also a concern. Admittedly, many correlative models also have large numbers of parameters, but these parameters are estimated from the data rather than specified by assumption a priori.

Free and open access to software with which to conduct such explorations is also a major consideration. That is, in contrast to modelling tools for correlational approaches, no software package for mechanistic modelling is, as yet, openly and freely available to the scientific community, at least to our knowledge. Moreover, mechanistic approaches require linkage of two rather complex model types: one to identify the key physiological features of an organism and the other to scale from millimetres to kilometres; again, neither challenge is trivial and, neither model has been made openly and freely available.

3.4. What should we be doing?

We can perhaps sketch out an imaginary case in which we assemble an 'ideal' approach to understanding the distributional ecology of a species. The fundamental niche could be estimated via physiological studies and mechanistic modelling. Ideally, though, the mechanistic modelling would be subjected to checks and modifications based on correlative models of the same species (see, e.g., Barve et al. 2014), and geographic assessments, to assure that a single 'niche' suffices for the species in question across its geographic range.

Once a niche estimate is in hand, however, we can then combine and integrate it with dispersal models providing an **M**-educated view of the distributional potential of the species. Specifically, beyond just simple maximum dispersal ranges, dispersal can and should be involved as a function of landscape and environmental features such that dispersal is not just the 'ink blot' spreading in a pool of water (Villalobos et al. 2014). By the same token, transient views of environmental changes through time that are of interest can be included, which will interact in complex ways with dispersal ability as populations diffuse across a changing environmental landscape. Such an ideal case has not, to our knowledge, been developed fully, although a few studies have linked multiple pieces of this complicated puzzle (Dormann et al. 2012; Kissling et al. 2012; Marion et al. 2012; Barve et al. 2014).

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