

Defining, estimating, and understanding the fundamental niches of complex animals in heterogeneous environments

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Abstract

During the past century, the fundamental niche, the complete set of environments that allow an individual, population, or species to persist, has shaped ecological thinking. It is a crucial concept connecting population dynamics, spatial ecology, and evolutionary theory, and a prerequisite for predictive ecological models at a time of rapid environmental change. Yet, its properties have eluded quantification, particularly for mobile, cognitively complex organisms. These difficulties are mainly a result of the separation between niche theory and field data, and the dichotomy between environmental and geographical spaces. Here, I combine recent mathematical and statistical results linking habitats to population growth, to achieve a quantitative and intuitive understanding of the fundamental niches of animals. I trace the development of niche ideas from the early steps of ecology to their use in modern statistical and conservation practice. I examine how animal mobility and behavior may blur the division between geographical and environmental space. I discuss how the central models of population and spatial ecology lead to a concise mathematical equation for the fundamental niche of animals and demonstrate how fitness parameters can be understood and directly estimated by fitting this model simultaneously to data on population growth and spatial distributions. I first illustrate these concepts theoretically for territorial species. I then fit the fundamental niche model to a data set of house sparrow colonies to quantify how a species of selective animals can increase their fitness in heterogeneous environments. This work confirms ideas that had been anticipated in the historical niche literature. Specifically, within traditionally defined environmental spaces, habitat heterogeneity and behavioral plasticity make the fundamental niche more complex and malleable than was historically envisaged. However, once examined in higher-dimensional environmental spaces, accounting for spatial heterogeneity, the niche is more predictable than recently suspected. This re-evaluation quantifies how organisms might buffer themselves from change by bending the boundaries of viable environmental space and offers a framework for

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designing optimal habitat interventions to protect biodiversity or obstruct invasive species. It therefore promotes the fundamental niche as a key concept for understanding animal responses to changing environments and a central tool for environmental management.

KEYWORDS

accessibility, *E*-space, fitness, habitat, population ecology, realized niche, spatial ecology, species distribution models, zero-niche paradox

INTRODUCTION

The broader idea of the niche, the correspondence between an organism and its biotic or abiotic environment, is a cornerstone of ecology (McInerney & Etienne, 2012a; Parentoni Martins, 2017; Sales et al., 2021) and holds wider prominence, in areas as diverse as evolutionary theory (Carscadden et al., 2020), cell biology (Pocheville, 2015), anthropology (D'Errico et al., 2017), law (Pedruski et al., 2016), and economics (Tisdell & Seidl, 2004). Its scientific significance lies in its potential to unify the subfields of spatial ecology, population dynamics, and evolution (Slack, 2011). Yet, despite its promise and prevalence in the literature (Parentoni Martins, 2017; Pedruski et al., 2016), the niche remains one of the most ambiguous terms in ecology (Hurlbert, 1981; Parentoni Martins, 2017; Sales et al., 2021). Perhaps, to achieve a robust definition of the niche, we must first aim for a convergence between the three ecological sub-fields that it adjoins.

The formative work by Hutchinson (Hutchinson, 1957, 1978) had set a course in this direction, by focusing on the fundamental niche, the part of environmental space that gives individuals of a species positive fitness and allows populations of the species to grow (Chase & Leibold, 2003; Peterson et al., 2011). This definition implicitly connects the environmental attributes of space to the viability of populations and the fitness of their members (Colwell & Fuentes, 1975), hence weaving together the necessary threads of spatial, population, and evolutionary ecology.

Akin to a Platonic ideal (Parentoni Martins, 2017), the fundamental niche is never observed directly, despite its compact definition. Instead, its various indirect manifestations, the realized niches, are observed in the distributions of species across landscapes (Colwell & Fuentes, 1975; Pulliam, 2000; Zurell et al., 2012). Realized niches differ from the fundamental niche because the correspondence between habitat suitability and species distributions is never exact (Cassini, 2011; Colwell & Rangel, 2009; Diez et al., 2014; Godsoe, 2012; Matthiopoulos, Fieberg, & Aarts, 2020; Pulliam, 2000). For example, species are often absent from suitable habitat due to dispersal limitations or historical artifacts (Hargreaves et al., 2014).

Conversely, species can be encountered in unsuitable habitat due to spillover of individuals from source habitats into neighboring sink habitats. Furthermore, the fundamental niche may include habitats that are not currently present anywhere in geographical space, so it is not possible to know by direct observation that such habitats would be suitable.

This conspicuous mismatch between the fundamental niche and observed species distributions has led to recurrent debate about its utility and, even, calls for its abandonment (Angilletta et al., 2019; Araújo & Guisan, 2006; Chase & Leibold, 2003; Chesson, 1991; Hubbell, 2004; McInerney & Etienne, 2012a, 2012b, 2012c). Suggestions for a more pragmatic approach (McInerney & Etienne, 2012c) argue that the niche concept is purely a conversational device and that an unambiguous understanding of the term is not a prerequisite for modeling the associations between species and habitats. However, this may be setting a low bar for the science of ecology (Parentoni Martins, 2017) because, although the fundamental niche is not essential for building *descriptive* models of where species are today, it is indispensable for *predicting* where they could occur (Yates et al., 2018; Zurell et al., 2012). At a time of rapid environmental change, describing the status quo with species distribution models is not enough, and the scarcity of predictive, transferable models is becoming an urgent problem for conservation and pest management (Mouquet et al., 2015). Perhaps that is why anticipatory studies on species' global ranges, invasion potential, critical habitat, and fine-scale habitat suitability, are often discussed in terms of individual fitness and population viability, the defining notions of the fundamental niche (Warren, 2012). A more formal understanding of the fundamental niche would crystallize these concepts and help us develop predictive models that can yield robust forecasts and biological insights about species distributions, range expansions, and extinctions (Kearney & Porter, 2004; Pulliam, 2000; Soberón, 2014; Soberón & Peterson, 2020; Yates et al., 2018). Our undisputed need to understand the viability of species in changing landscapes (Araújo & Guisan, 2006; Godsoe et al., 2017) means that "the niche is here to stay" (Soberón, 2014).

A considerable body of conceptual work has detailed the distinctions between habitat suitability and observed species distributions (Chase & Leibold, 2003; Godsoe, 2010; Holt, 2009; Peterson et al., 2011; Soberón, 2007; Soberón & Nakamura, 2009; Soberón & Peterson, 2005). For example, the BAM diagram (Soberón, 2007; Soberón & Nakamura, 2009; Soberón & Peterson, 2005) has become an essential way to organize our thinking on the relationship between species niches and geographic distributions. This increasing clarity must now be converted into more utilitarian definitions of the fundamental niche that can be estimated from data and used for real applications (Araújo & Guisan, 2006; Jimenez & Soberón, 2021). To achieve this utility, we need to address three knowledge gaps.

First, we require a general mathematical framework linking the fundamental to the realized niche. That is not to say that we have a shortage of “niche models” in the literature. Unfortunately, the indiscriminate use of the term “niche modeling,” often in *lieu* of species distribution modeling (SDM) has been counter-productive (McInerney & Etienne, 2013; Soberón, 2014; Warren, 2012). SDMs are models fitted to abundance/occurrence data and hence best-suited to mapping the density of populations at pseudo-equilibrium (i.e., to model the realized niche; see section 2 in Guisan & Zimmermann, 2000). They can only ever quantify the intrinsic growth rates of populations (i.e., the fundamental niche; Pagel & Schurr, 2011) under unrealistically strict conditions (Matthiopoulos, Fieberg, Aarts, et al. 2020). As long as the realized and fundamental niches are casually confused in this way, concepts that depend on them will also remain confused (Elith & Graham, 2009; Parentoni Martins, 2017; Soberón & Nakamura, 2009; Whittaker et al., 1973), endangering accurate ecological inference and prediction.

Second, we have few statistical frameworks for estimating the fundamental niche empirically (Blonder, 2018; Godsoe et al., 2017; Jiménez et al., 2019; McInerney & Etienne, 2012a; Pulliam, 2000), and none that specifically refer to vagile and selective animals. The batch of statistical methods typically named “niche models” (e.g., Broennimann et al., 2012; Drake et al., 2006; Hirzel & Arlettaz, 2003; Rotenberry et al., 2006; Thuiller et al., 2004) use presence-only data as a proxy for population viability. Their premise is that, if a species is found at a particular habitat, then the habitat must belong to its fundamental niche. This assumption will be untrue for sink populations. Furthermore, the interpretation of vacant habitats makes all the difference for our inferences about the niche. Is a habitat ostensibly unoccupied because the species has not yet colonized it, because it does not physically exist so as to be colonized, or because

our surveys have not actively looked for the species in that habitat? We need to know, not only what habitats the animals are found in, but also what options were accessible to them, and how well they are doing there. Presence-only methods are statistically weak, estimating niche-related objects that are found “at some unspecified point along a continuum between the fundamental and the realized niche” (Colwell & Rangel, 2009; Jiménez-Valverde et al., 2008; Peterson et al., 2011; Soberón & Peterson, 2005). Niche models that examine abundance or occupancy without corresponding measures of survey effort, habitat availability and population growth (Aldridge & Boyce, 2008; DeCesare et al., 2014), are of limited utility in an explanatory or predictive capacity (Pagel & Schurr, 2011; Schurr et al., 2012).

Third, the above two gaps have limited our intuition about the shape and boundaries of the fundamental niche. Since its inception, it has been imagined as a bounded (i.e., limited) and convex hypervolume in n -dimensional environmental space (Blonder, 2018; Blonder et al., 2014; Holt, 1987; Hutchinson, 1957; Malanson, 1997; Whittaker et al., 1973). This image stems from the original descriptions of the fundamental niche in terms of morphological or physiological tolerances (e.g., temperature envelopes; Kearney & Porter, 2004) that define simple ranges along each niche dimension. However, it is becoming apparent that the structure of fundamental niches may be more complex (Blonder, 2016; Soberón & Peterson, 2020). In particular, it has recently been postulated that environmental heterogeneity and phenotypic plasticity make the boundary of the fundamental niche “fuzzy” (Angilletta et al., 2019). This apparent stochasticity may stem from the fact that Hutchinsonian spaces, using mean environmental variables as their dimensions, are not complex enough to map fundamental niches, particularly for organisms that can sense heterogeneity and move selectively between different habitats.

Here, I address all three of these challenges. I synthesize recent theoretical results into a general, concise expression for the boundary of the niche that is both mathematically tractable and statistically estimable from field data. My approach relies on developing explicit expressions for population growth across spatial scales, that realistically accommodate spatial processes. I illustrate this statistical approach using both hypothetical scenarios and wildlife data. Using these motivating examples, I review our current intuition about the fundamental niche. By doing so, I suggest how to estimate the extent of endurance of plastic organisms, living in heterogeneous environments, in apparently inviable regions of niche space. Finally, I discuss how this framework can be extended and how this knowledge might help us resolve challenging human–wildlife conflicts.

FROM *G*-SPACES TO *E*-SPACES AND BACK AGAIN

The separation of physical from environmental space, known as Hutchinson's duality (Colwell & Rangel, 2009), was a source of considerable clarity in the golden age of niche theory (Pocheville, 2015; Sales et al., 2021), but has increasingly become a source of confusion as niche concepts have moved from the hypothetical realm, closer to field data and statistical methodology (McInerney & Etienne, 2012a; Parentoni Martins, 2017; Sales et al., 2021). A solid foundation for niche theory requires us to clearly define these spaces and recognize the relationship between them.

Geographical space (*G*-space) comprises the three physical dimensions of latitude, longitude, and altitude. A location $\mathbf{s} = (\text{Lat}, \text{Lon}, \text{Alt})$ in *G*-space may have n characteristics, such as scene-setting conditions (e.g., aspects of geomorphology, climate, and soil composition), resources (e.g., amount of food, number of breeding sites), or risks (e.g., exposure to predators or pollution). These n variables form the dimensions of environmental space (*E*-space). Since Hutchinson (Hutchinson, 1957), this is also known as "niche space," because he envisaged the fundamental and realized niches as subsets of *E*-space. Arguably, the extension of the niche to include resources (such as prey) and risks (such as predators or competitors) is a step away from Hutchinson's predominantly scenopoetic environmental variables but is a necessary consideration if we ultimately wish to move the fundamental niche to include dynamical interactions between species (see *Future developments: Mechanistic content of models leading to the niche*).

A point $\mathbf{x} = (x_1, \dots, x_n)$ in *E*-space uniquely defines a local environment, or habitat (Aarts et al., 2008; Hall et al., 1997; Matthiopoulos et al., 2011). Habitat availability refers to the composition of the environment that is accessible to an individual or group. Quantifying the availability $f_{\mathbf{x}}$ of a particular habitat \mathbf{x} depends on how finely habitats are classified and how accessible they are from the position of the study organisms (Martin et al., 2008; Matthiopoulos, 2003; Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020). We can initially think of availability $f_{\mathbf{x}}$ as the proportion of area of the accessible range of the individual or group, occupied by habitat \mathbf{x} . This requires us to think of habitats as finite volumes (rather than infinitesimal points) in *E*-space, so that it makes sense to measure the area they occupy in *G*-space (if habitats were classified with infinite precision, then the area occupied by each would be zero). It also assumes, that any point in *G*-space is either fully or not at all accessible to the organism. However, neither of these assumptions are necessary if we think of availability as a probability density. Relaxing these

assumptions leads naturally to infinitesimal definitions of habitat where availability decays smoothly with decreasing accessibility (Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020). Therefore, the availability scalar field \mathbf{f} is a probability density function such that $\int_E f_{\mathbf{x}} d\mathbf{x} = 1$.

Several of the published approaches to spatial heterogeneity have used convolutions of spatial kernels (e.g., Snyder and Chesson (2004); Chesson and Lee (2005); Jongejans et al. (2008)), or reaction–diffusion formulations (e.g., Nisbet and Gurney (2004); Skellam (1951)). These are all formulations in *G*-space that capture proximity in an explicitly spatial way. Spatial autocorrelation in covariates and limitations in mobility mean that geographical proximity and environmental proximity are connected (similar habitats are accessible from the current habitat $\mathbf{x}(\mathbf{s})$ at position \mathbf{x}). However, the complexity of objects in geographical space is commonly much higher than the complexity in environmental space (see figure 1 in Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020). Exploiting this property, the formulations of accessibility used here (developed in Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020) aim to simplify the treatment of proximity by examining neighborhoods in *E*-space. So, it is worth stressing that the integrals and definitions of usage and availability in the ensuing sections are over *E*-space, not *G*-space.

Figure 1 visualizes the correspondence between *G*- and *E*-spaces and prompts three important points. First, several very different landscapes can be constructed by rearranging the same ingredients (e.g., total amounts of resources) in *G*-space (e.g., compare Figure 1a,b). Second, the shape of habitat availability clouds in *E*-space can be very complex (Soberón & Nakamura, 2009), even including discontinuities and holes (Blonder, 2016). This makes it difficult to approximate realistic availability clouds with multivariate, but unimodal, Gaussian functions in *E*-space (such as those in Austin, 1985; Malanson, 1997; Jiménez et al., 2019; Jimenez & Soberón, 2021). Third, availability clouds in Hutchinson's *E*-space hold no information about the spatial contiguity of habitats and are therefore unable to communicate the *geographical context* in which an organism finds itself. Hence, although only one *E*-cloud can be constructed from a given *G*-landscape, infinite landscapes can be constructed from an availability cloud in *E*-space (Colwell & Rangel, 2009; Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020; i.e., the transition from *G* to *E* is irreversible). Despite this limitation, *E*-spaces are more suitable as the domain of concise mathematical models for habitat availability, habitat preference and the fundamental niche, because each habitat occurs exactly once as a point in *E*-space, whereas it can occur at multiple locations of *G*-space (see figure 1 in Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020).

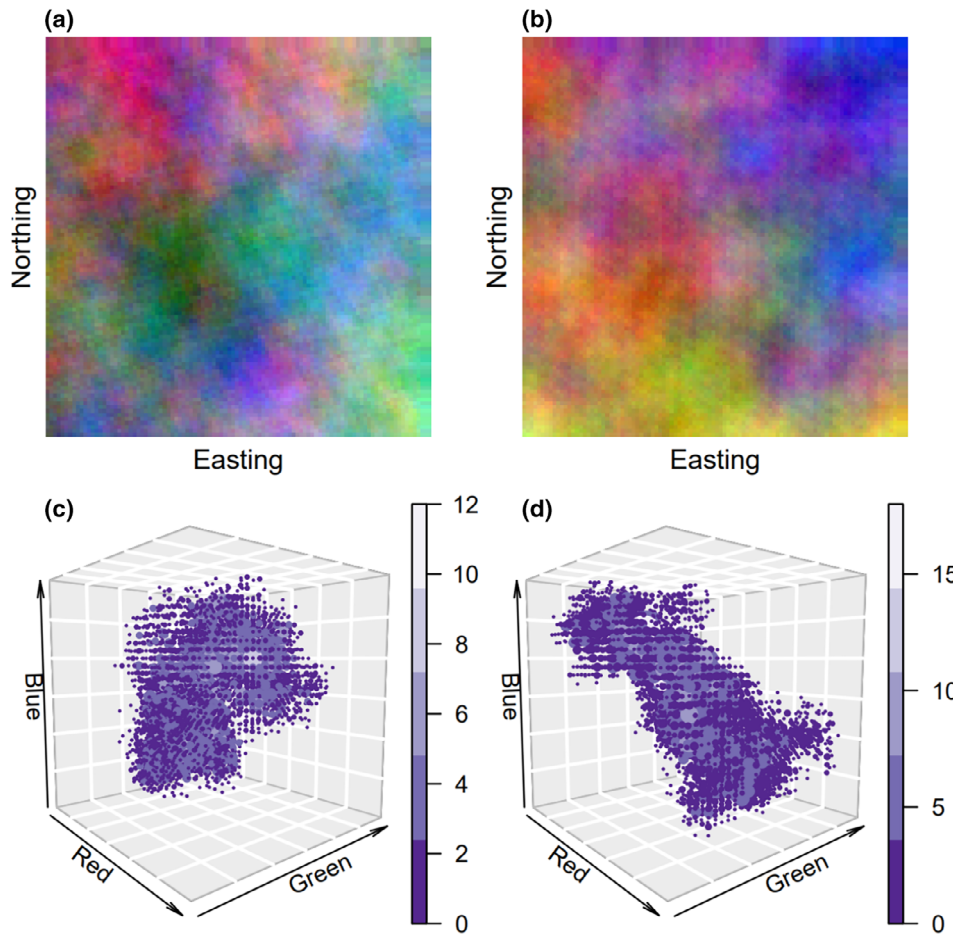


FIGURE 1 Illustration of geographical (*G*-space, top row) and environmental (*E*-space, bottom row) spaces. A *G*-space is a landscape, here mapped in the two dimensions of Easting and Northing. Two such landscapes (panels (a) and (b)) were created by mixing similar total amounts of three environmental variables. Each environmental variable is represented by a primary color: red, green, or blue. As different intensities of the three primary colors overlap locally in (a) and (b), they create a wide variety of mixture colors, each symbolizing a different habitat. The three axes of *E*-space (panels (c) and (d)) represent these three environmental variables (primary colors) and each mixed color in *G*-space (a unique habitat type) is a point in the three-dimensional *E*-space. Recording a dot at a particular point in *E*-space implies that the corresponding habitat can be found within the landscape in *G*-space. The intensity of purple color in *E*-spaces (c) and (d) represents the availability of each habitat type, the frequency with which this exact combination of environmental values occurs in each of the two landscapes above. The more spherical shape of the availability cloud in panel (c), as compared to panel (d), is entirely the result of chance in the generation of the original landscapes. More symmetric clouds than (c), and more irregular clouds than (d), are possible, from mixing the same overall amounts of the three primary colors.

Traditionally (Blonder, 2018; Blonder et al., 2014; Holt, 1987; Hutchinson, 1957; Malanson, 1997; Whittaker et al., 1973), niches have been imagined as compact subsets of *E*-space, objects not dissimilar to the three-dimensional cloud in Figure 1c. Indeed, if an animal inhabiting Figure 1a divided its time equally between all points of that landscape, its realized niche would coincide with Figure 1c. However, there has always been confusion about whether to think of the fundamental niche as a subset of *E*-space or as a place, in *G*-space (Whittaker et al., 1973). This lingering confusion stems from the tenable notion that a point in *E*-space should not be considered in isolation from its geographical

context (Angilletta et al., 2019). For instance, a situation not currently modeled by the niche literature is that animals are routinely able to survive in niche spaces where no “single” point is sufficient for their survival and reproduction (Holt, 2009). I will tentatively call this the “zero-niche paradox.” Often, vital resources are mutually exclusive in space (e.g., at a fine spatial scale, water holes and grazing land cannot coincide), and vagile animals have to perform short commutes or longer-range migrations to satisfy all their life-history requirements (Dennis, 2010). By moving across heterogeneous landscapes, animals can experience different types of habitats, and by actively selecting to use some over others,

they demonstrate high levels of behavioral plasticity (Holt, 2009). If we imagine that the two landscapes in Figure 1a,b happen to be the home ranges of two animals from the same species, then habitat suitability and the resulting viability of these two individuals may differ, even though they have access to the same average amounts of resources. So, we must consider the animals' fitness in the light of their "entire" environmental profile (i.e., the whole clouds in Figure 1c,d), not merely any single point in E -space.

It may be argued that this is a problem of scale (Jackson & Fahrig, 2015; Levin, 1992; McGill, 2010) and that summarizing (for instance, averaging) the environmental variables at spatial resolutions comparable to the home range of individuals (Cassini, 2011) may restore the concept of the fundamental niche to its classic form (i.e., mapping viability to single points in E -space). However, home ranges with the same average habitat composition can be very different indeed and heterogeneity around the average composition offers opportunities that can turn negative fitness into positive. Spatial and temporal heterogeneity will generally affect the viability of an organism (Holt, 2009; McLoughlin et al., 2006; Morales et al., 2010) so habitat homogeneity, artificially created by averaging environmental variables at coarse spatial scales, prevents us from correctly representing species responses to habitat.

It is important therefore to ask whether the existence of such heterogeneities, and the complex responses of animals to them, require us to modify our intuitive understanding of the fundamental niche. Does the ubiquitous fact that animals can move and choose between habitats to meet their needs matter for the size, shape and predictability of their fundamental niche? Below (*Example 2: House sparrows in suburbia and Necessary adjustments to our notion of the fundamental niche of animals*), I conclude that the answer is yes, even in E -spaces with three or fewer environmental variables, characterized by the most rudimentary forms of environmental heterogeneity.

POPULATION DYNAMICS IN E -SPACE

The fundamental niche has, at its heart, the concept of population viability, a core subject in population dynamics. So, it is useful to consider the niche from the viewpoint of population dynamics, defined within niche space (that is, a model that captures spatial heterogeneity not explicitly, as a landscape in G -space, but implicitly through the availability of different habitats to a species in E -space). At the same time, not all aspects of population dynamics will be relevant to the definition of the

niche, so it is useful to simplify the full population dynamics approach to a minimal set of necessary features. The full model presented in this section serves as an illustration of the assumptions made to arrive at the niche, rather than a key objective of the analysis presented later.

To begin with, consider a population of total size N_t living in an expansive and heterogeneous landscape of area A , much larger than the range of any single population member. Within each unit of habitat (\mathbf{x}), population size ($N_{\mathbf{x},t}$) can grow at a rate ($r_{\mathbf{x}}(N_{\mathbf{x},t})$) characteristic of that habitat, and the habitats around it. The local growth rate will also be dependent on population density in that habitat. The change in numbers within a habitat unit will also be affected by long-range immigration and emigration between habitats. A model in discrete time, defined in the corresponding E -space of that landscape might take the following form:

$$N_{t+1} = A \int_E \left\{ \underbrace{N_{\mathbf{x},t} f_{\mathbf{x}} r_{\mathbf{x}}(N_{\mathbf{x},t})}_{\text{Growth}} + \underbrace{f_{\mathbf{x}} \int_E g_{\mathbf{y} \rightarrow \mathbf{x}} N_{\mathbf{y},t} f_{\mathbf{y}} d\mathbf{y}}_{\text{Immigration}} - \underbrace{N_{\mathbf{x},t} f_{\mathbf{x}} \int_E g_{\mathbf{x} \rightarrow \mathbf{y}} f_{\mathbf{y}} d\mathbf{y}}_{\text{Emigration}} \right\} d\mathbf{x} \quad (1)$$

where $g_{\mathbf{y} \rightarrow \mathbf{x}}$ defines the per capita flux from a unit of habitat \mathbf{y} to one unit of habitat \mathbf{x} . This flux term describes the connectivity between different habitat types and must therefore be determined from the statistical properties of the environment (i.e., spatial auto- and cross-correlation of habitat characteristics) as well as the mobility of the species.

Although the functions $r_{\mathbf{x}}$ and $g_{\mathbf{y} \rightarrow \mathbf{x}}$ are not yet defined, we can make the following simplifying assumptions about this model that ultimately will form part of the definition of the niche. So, for the purposes of defining the niche:

1. The spatial scale over which the niche is described should not be the arbitrary spatial scale enclosing a population because different population members may experience very different conditions. It should instead be comparable to the range of the individual member of the species. This implies a simpler model of the form

$$N_{\mathbf{x},t+1} = N_{\mathbf{x},t} r_{\mathbf{x}}(N_{\mathbf{x},t}) + \int_E g_{\mathbf{y} \rightarrow \mathbf{x}} N_{\mathbf{y},t} f_{\mathbf{y}} d\mathbf{y} - N_{\mathbf{x},t} \int_E g_{\mathbf{x} \rightarrow \mathbf{y}} f_{\mathbf{y}} d\mathbf{y}. \quad (2)$$

2. We are interested in the ability of a species to establish in a particular habitat. Therefore, although the

local growth rate r_x will eventually be influenced by crowding, the niche must be considered for very small population sizes, such that the local growth rate of the population corresponds to its intrinsic growth rate r_x

$$N_{x,t+1} = N_{x,t}r_x + \int_E g_{y \rightarrow x} N_{y,t} f_y dy - N_{x,t} \int_E g_{x \rightarrow y} f_y dy \quad (3)$$

3. Similarly, the net growth of populations in crowded habitats may not reflect the habitats' intrinsic quality when large numbers of individuals emigrate, so emigration rates need to be excluded from the niche definition.
4. Although long-range immigration can sustain animals in habitats that would not be viable in isolation, the fundamental niche should not include such sink habitats. Conversely, although there will generally be regions in space that have not been accessed by a species, even if they are suitable, we must assume that all habitats that can support a species have received colonization attempts.

These assumptions imply a much simpler model, where the interest is in the definition of the intrinsic growth rate of a species at or in the neighborhood of any given habitat,

$$N_{x,t+1} = N_{x,t}r_x. \quad (4)$$

AN INITIAL DEFINITION OF THE FUNDAMENTAL NICHE

For the purposes of species- or population-level models, the concept of absolute individual fitness (as a characteristic of a genotype or phenotype) is often generalized to populations, by linking the average fitness F across individuals to population growth, using general models of the form (e.g., equation 3.9 in Turchin, 2003)

$$\frac{N_{t+1}}{N_t} = \exp(F(\mathbf{f}, \mathbf{N}_t)) \quad (5)$$

in which the population's fitness is determined by the composition of the environment (\mathbf{f}) and density-dependent influences ($\mathbf{N}_t = \{N_t, N_{t-1}, \dots\}$). Equation (5) is merely a deterministic model for the mean of a distribution of individual fitnesses within a population. This ecological use of average fitness has been extensively discussed in the literature (Murray, 1985; Nur, 1984, 1987; Ollason, 1991; Stenseth, 1983) and Equation (5) has a long history of use in evolutionary models (Fisher, 1930; Lande, 1982; Roff, 2008). It also specifies a mathematical

link between the environment of a species and its ability to grow, hence allowing us to formalize the concept of the niche at a species level, rather than the level of the individual.

Hutchinson envisaged the fundamental niche of a species as the set of points \mathbf{x} in E -space yielding nonnegative intrinsic population growth (Chase & Leibold, 2003; Godsoe et al., 2017; Peterson et al., 2011; Soberón, 2007), allowing species members to invade and occupy these habitats (Peterson et al., 2011), in the absence of interspecific or intraspecific competition. Hence, each point in E -space was assumed to map to a single value of fitness for a founder (i.e., density-independent) population. We can obtain an expression that adheres to this definition of the fundamental niche by simplifying Equation (5) in two ways. First, we must specify it to near-zero population densities ($\mathbf{N}_t \approx \mathbf{0}$). A species at high densities may have zero or negative growth due to crowding effects, which is why population growth rates in high-density scenarios are not a good indicator of viability (McLoughlin et al., 2010). Arguably, density dependence may also affect the species at low densities, if it is subject to Allee effects (Courchamp et al., 1999) and further work will be required to extend Hutchinson's definition to allow for these (Holt, 2009; Holt et al., 2004). The second simplification of Equation (5) is to specify it to the fitness generated by a single habitat (i.e., to map fitness to a single point \mathbf{x} in E -space). Under the above two simplifications, growth rate will be (compare with Equation 4):

$$\frac{N_{t+1}}{N_t} = \exp(F(\mathbf{x})). \quad (6)$$

Then, Hutchinson's "fundamental niche" is a subset of E -space defined as

$$E_I = \{\mathbf{x} : F(\mathbf{x}) \geq 0\} \quad (7)$$

and the niche boundary is obtained by setting $F(\mathbf{x}) = 0$.

The utility of this mathematical definition for practical applications (such as animal conservation) is limited. First, the fitness of most mobile animals will be determined by not one, but several different habitats within accessible G -space. The above expression is written in E -space, which, as mentioned earlier cannot easily store the geographical proximity between habitats (Angilletta et al., 2019). Second, fitness and the availability of accessible habitats need to be written as mathematical functions so that their parameters can be estimated in real-world situations. For these reasons, the above definition is far removed from the spatial data (e.g., telemetry, transect survey, remote sensing) that quantify habitat availability and habitat use in real systems.

INDIVIDUAL VERSUS POPULATION NICHES

The fundamental niche is a concept usually associated with entire species, but its definition and subsequent estimation depend on how individuals experience and respond to their environment (Carscadden et al., 2020). Scaling up from the individual to the population niche requires us to think of four aspects of biology:

1. Individual variation: Phenotypic variation between individuals results in differences in their tolerances of environmental extremes. In effect, the niche of a species is the convolution between individual tolerances and between-individual variation (Roughgarden, 1974). The concept of fitness at the population level can be thought of as the average of individual fitnesses and the variation around this average. It is the material on which natural selection operates. Although, in this paper, I refer to a single measure of (average) fitness for the population, a genuine consideration of niche evolution would require the mathematical framework to be extended to include individual variation (Carlson et al., 2021).
2. Movement ecology: Although populations may be distributed across a landscape, not all population members will be able to experience the full distribution of environmental variables. Given that a population is made up of individuals, possibly residing at different parts of space, movement constraints deserve to be taken into consideration in scaling up from individuals to populations.
3. Spatial ecology: Environmental variables have nonuniform distributions, and different variables are characterized by unique levels of autocorrelation and cross-correlation. Therefore, each part of the landscape (within an individual's mobility constraints) will present a unique habitat composition. The fitness of a population will be the result of these unique experiences by its individual population members.
4. Behavioral ecology: Within the constraints of their genetic makeup, mobility, and position in the landscape, individuals will have unique behavioral responses to how they exploit their environment. Habitat selection is an important driver of individual fitness, and the emergent population fitness will be shaped by it.

ANIMAL MOBILITY AND THE NICHE

The main challenge in formalizing the niche concept for animals is that they are predominantly mobile organisms and that even primitive animals have perception and

cognitive control of their movements, such that they can actively select which habitats to use. Therefore, viability may not only depend on a single habitat \mathbf{x} (see zero-niche paradox, above). Spatial heterogeneity may offer animals different options within their accessible space. To associate fitness with a given habitat \mathbf{x} , we need to view it in the context of its surrounding habitats. For that purpose, we may interpret \mathbf{x} as the central vantage point from which an animal perceives this heterogeneous landscape. For example, \mathbf{x} may be the habitat characterizing the current location of a nomad in the landscape, or the habitat at the centroid of the home range of a central-place forager. Alternatively, it may be a statistical summary of an animal's surroundings, such as the average habitat within its home range. Ultimately however, \mathbf{x} is a reference habitat in E -space, around which we want to evaluate viability, in order to determine whether \mathbf{x} belongs to the fundamental niche, or not. Note that although this reasoning adds considerable realism to our existing models of habitat selection, in the future it would need to be further expanded to include migratory animals whose interannual viability relies on habitats separated by very large distances (Carscadden et al., 2020).

To quantify what habitats an animal experiences, we must therefore consider just how mobile it is and what habitats are likely to be available to it from its position. From the perspective of E -space, mobility determines the capacity of an organism to reach and use different habitats \mathbf{z} given that it is currently occupying a particular habitat \mathbf{x} , but this effect can only be captured by considering the proximity between habitats in G -space, for a particular landscape. If, at a geographical location \mathbf{s} , an animal encounters the habitat \mathbf{x} , we may be able to anticipate what types of habitat are likely to be available to it within its accessible neighborhood, given the size of that neighborhood and the characteristic spatial autocorrelation of habitats (Barve et al., 2011; Martin et al., 2008; Matthiopoulos, 2003; Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020). Therefore, an important aspect of the fitness $F(\mathbf{x})$ attained by an organism when it is located at a particular habitat \mathbf{x} , at a set of spatial coordinates \mathbf{s} , is that it depends on context (Angilletta et al., 2019), i.e., the habitat composition in the neighborhood of those coordinates. Because of this, it is necessary to distinguish between the context-specific version of fitness $F(\mathbf{x})$ and the context-independent fitness contribution of a single habitat, denoted here by $F_{\mathbf{x}}$, and defined as the long-term fitness characterizing a completely *sessile* individual constrained within habitat \mathbf{x} . For example, during the sessile stages of some animals (e.g., porifera and anthozoa), we can assume that $F(\mathbf{x}) = F_{\mathbf{x}}$. Similarly, when the mobility of an animal is small (e.g., echinoderms) compared to the heterogeneity of

their environment, we can assume $F(\mathbf{x}) \approx F_{\mathbf{x}}$, because animals may not be able to move fast enough to exit a particular habitat. Context-specific usage, denoted by $u_{z|x}$ is defined as the expected proportion of usage of a particular habitat \mathbf{z} , from a reference habitat \mathbf{x} . Context-specific usage is a function of both habitat availability and preference (as will be seen below) and can help express a relationship between context-specific and context-independent fitness:

$$F(\mathbf{x}) = \int_E F_{\mathbf{z}} u_{z|x} d\mathbf{z}. \tag{8}$$

The integral gives overall fitness $F(\mathbf{x})$ at \mathbf{x} as the usage-weighted average of habitat-specific fitness contributions $F_{\mathbf{z}}$, of all habitats across E -space. I consider context-independent fitness and context-specific usage (the two components of the integrand), in turn.

Context-independent fitness can be adequately represented by quadratic polynomials of habitat variables (Austin, 2007; Matthiopoulos et al., 2015)

$$F_{\mathbf{x}} = \sum_{k=1}^n \sum_{v=0}^2 \beta_{v,k} x_k^v \tag{9}$$

where the first sum is over n habitat variables and the second sum generates the quadratic polynomials with terms of order v .

Here, the values of the beta coefficients will depend on the ecological nature of the k th environmental variable. In particular, linear (hence, monotonic) terms may be used to describe responses to environmental resources ($\beta_{1,k} > 0, \beta_{2,k} = 0$) and risks ($\beta_{1,k} < 0, \beta_{2,k} = 0$) while downward-pointing parabolas can describe peaks in the responses to conditions ($\beta_{1,k} > 0, \beta_{2,k} < 0$). Two distinct components of fitness have been considered (Matthiopoulos et al., 2015), with and without the effect of density dependence. Although the density-dependent component must be included when fitting these models to population data, in defining the fundamental niche, we are interested in the population’s intrinsic growth rate (see *Population dynamics in E-space* and *An initial definition of the fundamental niche*), which can be obtained from the density-independent part of the model (assuming no Allee effects are in operation at small population sizes).

The context-specific habitat usage component $u_{z|x}$ in Equation (8) may be expressed as a function of habitat preference and habitat availability. This approach is taken by a broad class of methods under the collective name of Habitat Selection Functions (HSFs), a term previously introduced (Aarts et al., 2013; Matthiopoulos et al., 2015; Paton & Matthiopoulos, 2018) with reference to the most popular inferential approaches such as

Maximum Entropy (MaxEnt; Elith et al., 2011, Merow et al., 2013) and Resource Selection Functions (RSFs; Boyce & McDonald, 1999, Manly et al., 2002). Habitat selection originates from the idea of disproportionate use, compared to the availability of a habitat (Johnson, 1980). Therefore, a habitat-selection function is defined in terms of usage per unit of habitat available

$$w_{z|x} \propto \frac{u_{z|x}}{f_{z|x}}. \tag{10}$$

This expression is most often encountered in its unconditional form $w_{\mathbf{z}} \propto \frac{u_{\mathbf{z}}}{f_{\mathbf{z}}}$ (Boyce & McDonald, 1999). However, the biological interpretation of an unconditional formulation is unrealistic, because it either implies that the animal has uniform access to the entire landscape, no matter how large that is (Manly et al., 2002), or that the range of a single individual contains a completely representative sample of the broader landscape. Equation (10) implies a definition for context-specific habitat usage (Lele & Keim, 2006)

$$u_{z|x} = \frac{w_{z|x} f_{z|x}}{I_{\mathbf{x}}} \tag{11}$$

where the denominator is a normalizing integral $I_{\mathbf{x}} = \int_E w_{z|x} f_{z|x} d\mathbf{z}$ ensuring that usage across E -space sums to 1. Animal mobility and behavior can complicate our formulations of both determinants of usage in Equation (11), so the notions of habitat availability and habitat preference are developed in the next two sections, with attention to biological realism.

MOBILITY AND HABITAT AVAILABILITY

Given a reference habitat \mathbf{x} , the availability ($f_{z|x}$) of other habitats \mathbf{z} in the surrounding landscape will depend on spatial structuring and the mobility of the organism (Matthiopoulos, Fieberg, Aarts, Barraquand, & Kendall, 2020). From this palette of available habitats, animals choose to use some more than others.

The simplicity of the definition of habitat availability $f_{\mathbf{x}}$ as the amount (e.g., total area) of a habitat that is accessible to a population is deceptive, because it does not easily yield to quantification for a given species in a given landscape. As shown by a number of earlier studies (Aarts et al., 2013; Barve et al., 2011; Beyer et al., 2010; Martin et al., 2008; Paton & Matthiopoulos, 2018), the quantitative representation of what is available to animals can alter the parameter estimates and predictions of such models, often converting underlying preference to apparent avoidance of particular habitats, and vice versa.

This makes the definition of habitat availability one of the most challenging and influential steps of SDM development. Two aspects of movement, in particular, require attention. The first refers to accessibility of any point in E -space from another, and the second relates to complementary use of habitats by means of commuting.

Dealing with accessibility between habitats \mathbf{z} and \mathbf{x} , requires us to port geographical measures such as mobility and spatial autocorrelation into E -space. However, to manipulate habitat availability mathematically, we first need to represent it parametrically, as a function of statistical summaries of environmental composition. Habitat availability across an arbitrarily large geographical domain, may be approximated in n environmental dimensions by a Gaussian mixture of L components (Matthiopoulos et al., 2015). Each Gaussian component represents a kernel of high availability (a hot spot) centered at a particular location in E -space, and the different components are combined (mixed) according to different weights, to generate complex clouds of availability

$$f_{\mathbf{x}} = \sum_{l=1}^L \psi_l f_{l,\mathbf{x}} \quad (12)$$

$$= \frac{1}{(2\pi)^{\frac{n}{2}} \prod_{k=1}^n \sigma_k} \sum_{l=1}^L \psi_l \exp\left(\frac{1}{2} \sum_{k=1}^n \left(\frac{x_k - \mu_{l,k}}{\sigma_k}\right)^2\right)$$

where $f_{l,\mathbf{x}}$ is the l th mixture component (a unimodal probability density function in n dimensions), ψ_l is the weight associated with the l th component (such that $\sum_{l=1}^L \psi_l = 1$), $\mu_{l,k}$ is the mean (i.e., the location in E -space) of the l th mixture component along the k th environmental dimension, and σ_k is the characteristic standard deviation along the k th environmental dimension. This form of context-independent availability, defined in E -space, gives us the probability density of any given habitat \mathbf{x} across the whole of G -space. This Gaussian mixture approximation is not the only way to formalize n -dimensional hypervolumes, but all other available approaches are similar in spirit (Blonder et al., 2014). In general, these are approximation methods that create smoothed clouds of availability based on environmental data. Smoothing in E -space produces increments of availability in habitats that may not be physically present in the area of data collection. Like all smoothing methods, there is a trade-off between the flexibility of the smoother (e.g., number of parameters) and the degree of detail from the data that can be emulated. In the Gaussian mixture approach above, the higher the number of components used for fitting to the data, the better the approximation of the actual availability cloud and the lower the degree of smoothing (but smoothing may not necessarily be undesirable, as I discuss at the end of this section).

We can extend these ideas to define context-specific availability $f_{\mathbf{z}|\mathbf{x}}$, which describes the frequency with which different habitats \mathbf{z} would be accessible close to a reference habitat \mathbf{x} and depends on organism mobility and environmental autocorrelation. Recently, an expression was derived (Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020) for context-specific habitat availability for orthogonal environmental variables (i.e., either raw environmental variables presenting no cross-correlation, or rotated covariates via a method such as principal components analysis), as perceived from the vantage point of an organism found at habitat \mathbf{x} . This expression describes the habitats likely to be encountered by an organism conditional on the habitat \mathbf{x} where the organism is centering its usage. Intuitively, this is a localized model of availability, written in terms of the global Gaussian mixture components

$$f_{\mathbf{z}|\mathbf{x}} = \prod_{k=1}^n f_{\mathbf{z}_k|\mathbf{x}_k} \quad (13)$$

$$= \prod_{k=1}^n \frac{1}{f_{\mathbf{x}_k}} \sum_{l=1}^L \sum_{m=1}^L \Psi_{k,l,m} f_{l,\mathbf{x}_k} f_{m,\mathbf{z}_k}$$

where, as in Equation (12), f_{l,\mathbf{x}_k} , f_{m,\mathbf{z}_k} are respectively the l th and m th Gaussian components for the k th environmental dimension at the values \mathbf{x} , \mathbf{z} . The Gaussian mixture $f_{\mathbf{x}_k}$ at the value \mathbf{x} of the k th variable is calculated using the new weights $\Psi_{k,l,m}$ that are derived as a function of the mobility of the study organism combined with empirical curves of the spatial autocorrelation of the environmental covariates (see Appendices in Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020).

The formulations of $f_{\mathbf{z}|\mathbf{x}}$ can describe much more complex availability clouds in E -space, than those shown in Figure 1c,d, but can also represent the contiguity and structure of habitats in G -space (Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020). In addition, $f_{\mathbf{z}|\mathbf{x}}$ contains information about the mobility of the organism, enabling it to capture the scale at which a typical individual experiences the ambient heterogeneity in its environment. Implicit information on these two quintessentially geographical properties (habitat contiguity and animal mobility) allows the integral over E -space in Equation (8) to capture the habitat context around \mathbf{x} .

Although originally proposed to account for spatial structuring, this model can readily be extended to represent temporal structuring (e.g., trend, stochastic, or seasonal components). This can extend the notion of viability to temporal change (Soberón & Peterson, 2020), accounting for aspects of plasticity displayed by sessile, but temporally varying organisms, such as plants.

A feature of this framework not yet fully explored is complementarity in habitat use, which leads to the

“zero-niche paradox” mentioned in *From G-spaces to E-spaces and back again*. If an organism can commute between multiple habitats, it can use their properties in a complementary way. For example, a habitat that provides water and one that provides food may be insufficient for survival, on their own, but entirely adequate to support an organism when used in combination. By commuting, an animal effectively experiences a third, sufficient habitat (containing both water and food). This can be thought of as the capacity of mobile organisms to alter habitat availability, depending on spatial context, i.e., the total set of habitats that physically exist and are within reach of an organism (Angilletta et al., 2019). The above approach, constructing Gaussian approximations of observed availabilities, has the potential to capture complementarity by smoothing these observed frequencies into approximate probability densities. Through this local averaging operation, habitats that may not physically exist, but are similar to combinations of several extant habitats, receive a non-zero availability, hence allowing the framework to emulate complementary use by animals. Although more research is needed to determine how this smoothing operation could faithfully capture complementarity between habitats, it is important to stress the expandability of the approach presented here. By redefining habitat availability in this way, we would not need to alter any other aspects of the statistical frameworks reviewed in the following section.

MOBILITY AND HABITAT PREFERENCE

Habitat preference ($w_{z|x}$) can capture variations in usage due to animal behavior (Matthiopoulos et al., 2011). Following the requisites of HSF frameworks, such as Maximum Entropy (MaxEnt; Elith et al., 2011; Merow et al., 2013) and Resource Selection Functions (RSFs; Boyce & McDonald, 1999; Manly et al., 2002), habitat preference is broadly expressed as an exponential transformation of a predictor function $g(\mathbf{x})$

$$w_{z|x} = \exp(g(\mathbf{x})). \tag{14}$$

Echoing the formulation for context-independent fitness in Equation (9), the predictor function $g(\mathbf{x})$ can be formulated as a second-order polynomial in the dimensions of the vector \mathbf{x} , for some coefficients γ . The coefficients $\gamma_{v,k}$ of habitat preference are not the same as the fitness coefficients $\beta_{v,k}$ in Equation (9) because apparent habitat suitability can be context-specific (Arthur et al., 1996; Gillies et al., 2006; Mysterud & Ims, 1998), whereas the coefficients of fitness should be fixed for any given animal

$$w_{z|x} = \exp\left(\sum_{k=1}^n \sum_{v=0}^2 \gamma_{v,k} x_k^v\right). \tag{15}$$

There is an extensive literature describing how the use of a particular habitat can be affected nonlinearly by the availability of surrounding habitats, a phenomenon called a functional response in habitat selection (Holbrook et al., 2019; Mysterud & Ims, 1998). To resolve this, it was suggested (Boyce et al., 1999) that functional responses could be flexibly captured by expressing the γ coefficients of Equation (15) as functions of the entire habitat availability field $\gamma(\mathbf{f})$. Such varying coefficient models have existed in spatial statistics for some time (Hastie & Tibshirani, 1993), and their application in ecology is becoming more widespread (Barnett et al., 2021; Osborne et al., 2007), but for functional responses, the local dependence is with reference to the habitat composition of a particular region of a landscape. In its simplest form, a varying coefficient may be written as a linear combination of the availabilities of all habitats across E -space, for a particular landscape

$$\gamma_{v,k} = \int_E \eta(\mathbf{y}) f_{y,k} d\mathbf{y} \tag{16}$$

for some function η that describes how the coefficient γ responds to the availability of any given habitat \mathbf{y} . Specifically, η is the change in the slope of the v th order term of the k th environmental variable as a result of a unit-increase in the availability of habitat \mathbf{y} . The v, k , slope is the varying coefficient in relation to the v th-order polynomial term of the k th environmental variable. This varying-coefficient approach was named a Generalized Functional Response (GFR) (Matthiopoulos et al., 2011) and a particular version of GFRs was formulated, by expressing the η 's as polynomial functions of environmental variables. This is the simplest formulation of GFRs and leads to an expression for the coefficients of habitat preference, in terms of the moments (i.e., the j th-order expectations) of the marginal distributions of habitat availability along each environmental dimension

$$\gamma_{v,k} = \delta_{v,k,0} + \sum_{i=1}^n \sum_{j=1}^{\infty} \delta_{v,k,i,j} E[X_i^j]. \tag{17}$$

In practical applications, due to limitations in data availability, only the lower moments are used (i.e., the average value of each environmental variable in the neighborhood of the point of interest)

$$\gamma_{v,k} = \delta_{v,k,0} + \sum_{i=1}^n \delta_{v,k,i} \bar{X}_i. \tag{18}$$

The exploration of efficient (i.e., economical with degrees of freedom) and effective (i.e., accurate and precise) GFR models is still at its early stages and improvements of implementing the general idea of Equation (16) will be possible (Aldossari et al., 2021). However, currently the state of the art with GFRs is Equation (17), and this has repeatedly been able to improve the predictive abilities of HSF models (Aarts et al., 2013; Matthiopoulos et al., 2011, 2015, 2019; Muhly et al., 2019; Paton & Matthiopoulos, 2018).

PARAMETRIC DEFINITION OF THE FUNDAMENTAL NICHE

We now have all the necessary ingredients to construct a mathematical definition of the fundamental niche of animals that can be estimated from field data. The condition in Equation (7) can now be expanded with the aid of Equations (8) and (11)

$$\frac{1}{I_{\mathbf{x}}} \int_E F_{\mathbf{z}} w_{\mathbf{z}|\mathbf{x}} f_{\mathbf{z}|\mathbf{x}} d\mathbf{z} \geq 0.$$

Given that the normalizing constant $I_{\mathbf{x}}$ is consistently nonnegative, we can simplify the above expression into an equation for the boundary of the fundamental niche

$$\int_E F_{\mathbf{z}} w_{\mathbf{z}|\mathbf{x}} f_{\mathbf{z}|\mathbf{x}} d\mathbf{z} = 0. \quad (19)$$

The integral is proportional to the fitness $F(\mathbf{x})$ around a reference habitat \mathbf{x} . It aggregates all nearby habitat-specific contributions $F_{\mathbf{z}}$, weighted by the availability ($f_{\mathbf{z}|\mathbf{x}}$) of each habitat and by preferential usage ($w_{\mathbf{z}|\mathbf{x}}$) of habitats by members of the species.

The three quantities participating in the integral are estimable from field data. The habitat-specific fitness $F_{\mathbf{z}}$ has been formulated mathematically (Matthiopoulos et al., 2015) and fitted to combined space use and population growth field data (Matthiopoulos et al., 2019). This framework hybridizes spatial and demographic model fitting and is a specific example of the much broader class proposed conceptually by Schurr et al. (2012). The habitat preference model $w_{\mathbf{z}|\mathbf{x}}$, once recast as a GFR model (Matthiopoulos et al., 2011), can be estimated from usage data (Matthiopoulos et al., 2011, 2019). Finally, the context-specific availability can be derived from a flexible approximator, such as the Gaussian mixture model (Matthiopoulos et al. 2015; Matthiopoulos, Fieberg, Aarts, Barraquand, et al., 2020), as was described in *Mobility and habitat availability*.

Equation (19) relies on different categories of parameters. The function $F_{\mathbf{z}}$ contains the vector of “fitness

parameters” β , the function $w_{\mathbf{z}|\mathbf{x}}$ contains the vector of “habitat-use parameters” γ , and the function $f_{\mathbf{z}|\mathbf{x}}$ contains the “habitat availability” parameters, which in the case of Gaussian mixtures would principally be (μ, σ) , the weights, locations, and variances of the Gaussian mixture components. Equation (19) is not limited to the particular formulations mentioned above. Other types of functions may be devised to broaden the applicability of this very general framework to a wealth of life histories for different animals. As will be seen in the examples below (*Example 1: Territorial or colonial species* and *Example 2: House sparrows in suburbia*), for the cases of territorial, home ranging, or colonial species, it is possible to specify these functions and proceed with particular mathematical formulations of the niche.

The solutions of Equation (8) are not merely points in E -space, but fully parametric descriptions of entire landscapes that can offer the species neutral (i.e., zero) fitness. The equation has infinite solutions in its extended parameter space, which may have many more dimensions than E -space. These extra dimensions arise from the need to describe complex habitat availability distributions in E -space (using parameters to capture higher moments of resource distributions, such as variance, skewness, and outliers, but also multimodality). For example, for an E -space of n orthogonal environmental variables, allowing a trimodal marginal distribution of availability in each environmental dimension, results in a fundamental niche space of at least $4n$ dimensions (characterizing the positions of the three modes and an identical variance around each mode). Even in the case of unimodal availability (corresponding to n -dimensional ellipses in E -space), describing a heterogeneous environment requires twice as many dimensions as Hutchinson’s niche space. Only completely homogeneous environments can be sufficiently described by n environmental dimensions. This is not to say that the classical definition of E -space will not capture some points of the fundamental niche. It just means that this set of points will be contained within a larger set defined in a higher dimensional definition of E -space that allows us to describe environmental heterogeneity. Although impossible to visualize, solutions to this equation are entirely possible to retrieve. As will be seen in the house sparrow example below (see Equations 27 and 28), for some natural histories, it may even be possible to describe the fundamental niche using simple integral-free algebraic expressions.

However, for other biological scenarios, exhaustively describing the set of solutions by means of an algebraic expression may not be possible. In these cases, the present framework can always be used to calculate whether a particular landscape is inside or outside the niche

boundary (Godsoe, 2010). Such a “what-if” question would require us to numerically calculate the integral in Equation (8) and thus check whether it gives positive or negative values. Similar calculations could be used to quantify fitness and compare fitness values between two candidate landscapes. Such comparisons form the basis for all generic optimization, or Monte Carlo Markov Chain methods and are therefore the core for targeted ecosystem management (see *Future developments: Optimizing ecosystem management*).

EXAMPLE 1: TERRITORIAL OR COLONIAL SPECIES

By focusing on colonial or territorial species and assuming, for simplicity, equal accessibility of all points within the territory or home range, it is possible to describe availability of habitats to the animals via the simpler Gaussian mixture in Equation (12), instead of the conditional approximation of Equation (13), which deals with gradations in accessibility. Then, the integral of Equation (19) becomes

$$\int_E \sum_{k=1}^n \sum_{v=0}^2 \beta_{v,k} x_k^v \exp\left(\sum_{k=1}^n \sum_{v=0}^2 \gamma_{v,k} x_k^v\right) \times \sum_{l=1}^L \psi_l \exp\left(\frac{1}{2} \sum_{k=1}^n \left(\frac{x_k - \mu_{l,k}}{\sigma_k}\right)^2\right) dx = 0. \tag{20}$$

This expression has a closed form (see Appendix A in Matthiopoulos et al., 2015)

$$\sum_{l=1}^L \psi_l \Theta_l \sum_{k=1}^n \sum_{v=0}^2 \beta_{v,k} Z_{v,k} = 0 \tag{21}$$

where

$$\Theta_l = \prod_{k=1}^n \left(\frac{2\pi\sigma_k^2}{1 - 2\gamma_{2,k}\sigma_k^2}\right)^{\frac{1}{2}} \exp\left(\gamma_{0,k} - \frac{\mu_{l,k}^2}{2\sigma_k^2} + \frac{(\gamma_{1,k}\sigma_k^2 + \mu_{l,k})^2}{2\sigma_k^2(1 - 2\gamma_{2,k}\sigma_k^2)}\right) \tag{22}$$

and

$$Z_{0,k} = 1, Z_{1,k} = \frac{\gamma_{1,k}\sigma_k^2 + \mu_{l,k}}{1 - 2\gamma_{2,k}\sigma_k^2}, Z_{2,k} = \frac{\sigma_k^2}{1 - 2\gamma_{2,k}\sigma_k^2} \left(1 + \frac{(\gamma_{1,k}\sigma_k^2 + \mu_{l,k})^2}{\sigma_k^2(1 - 2\gamma_{2,k}\sigma_k^2)}\right). \tag{23}$$

Note that this expression is independent of \mathbf{x} . It depends purely on the parameters of fitness (β), habitat

availability (ψ, μ, σ), and habitat preference (γ). The fitness parameters are fixed (independent of habitat availability) and the habitat preference parameters depend on habitat availability (via a GFR, see Equation 18). Therefore, the fundamental niche boundary in this example depends solely on the habitat composition of the home range or territory. Ultimately, therefore, we can decide if a particular landscape composition within the territory (as determined by ψ, μ, σ) allows a typical animal from the species to have positive fitness.

To gain some intuition around these expressions, consider a hypothetical scenario (Figure 2) in which a territorial organism is affected by only one environmental variable x , so that $n=1$. Fitness of the organism is highest at intermediate values of the variable and extreme values of the variable are inviable (i.e., confer negative fitness, see Figure 2a). We assume that the organism has complete access to all points within its territory and the distribution of values of the environmental variable has a simple unimodal shape, so that the sole Gaussian component ($L=1, \psi_1=1$) is described by (μ, σ) (two examples of such availability profiles, named low- x and medium- x scenarios, are shown in Figure 2b). The habitat preferences (Figure 2c) are affected by a functional response, so that in the low- x scenario (red dashed curve in Figure 2b) the animal appears to show stronger preference for higher values of x (red dashed curve in Figure 2c). Following the GFR approach (Equation 18), the parameters of habitat preference for the linear and quadratic response to the single environmental variable can be written as linear functions of availability so that $\gamma_1 = \delta_{1,0} + \delta_{1,1}\mu, \gamma_2 = \delta_{2,0} + \delta_{2,1}\mu$.

Consequently, the animal can shift its usage (Figure 2d) of the environmental variable closer to the intermediate values of x . In G -space, in the low- x scenario, the animal would concentrate its usage to parts of the territory with intermediate values of x , but these parts would appear to be preferred more than the medium- x scenario. We can investigate the implications of this simple form of behavioral plasticity for the size of the niche, but first we need to decide on the dimensionality of the relevant niche space. For this example, the availability profile of the single variable is determined by two quantities, the mean and variance of the availability distributions in Figure 2b. These two values form the dimensions of the niche space. So, even though the Hutchinsonian E -space is one-dimensional, spatial variability in x values across the territory means that the niche space is two-dimensional. Figure 2e shows the shape of the fundamental niche in this two-dimensional space and the colors indicate the fitness of the animals living in these conditions. By specifying Equations (21)–(23) to the circumstances of this simple example, the boundaries of the

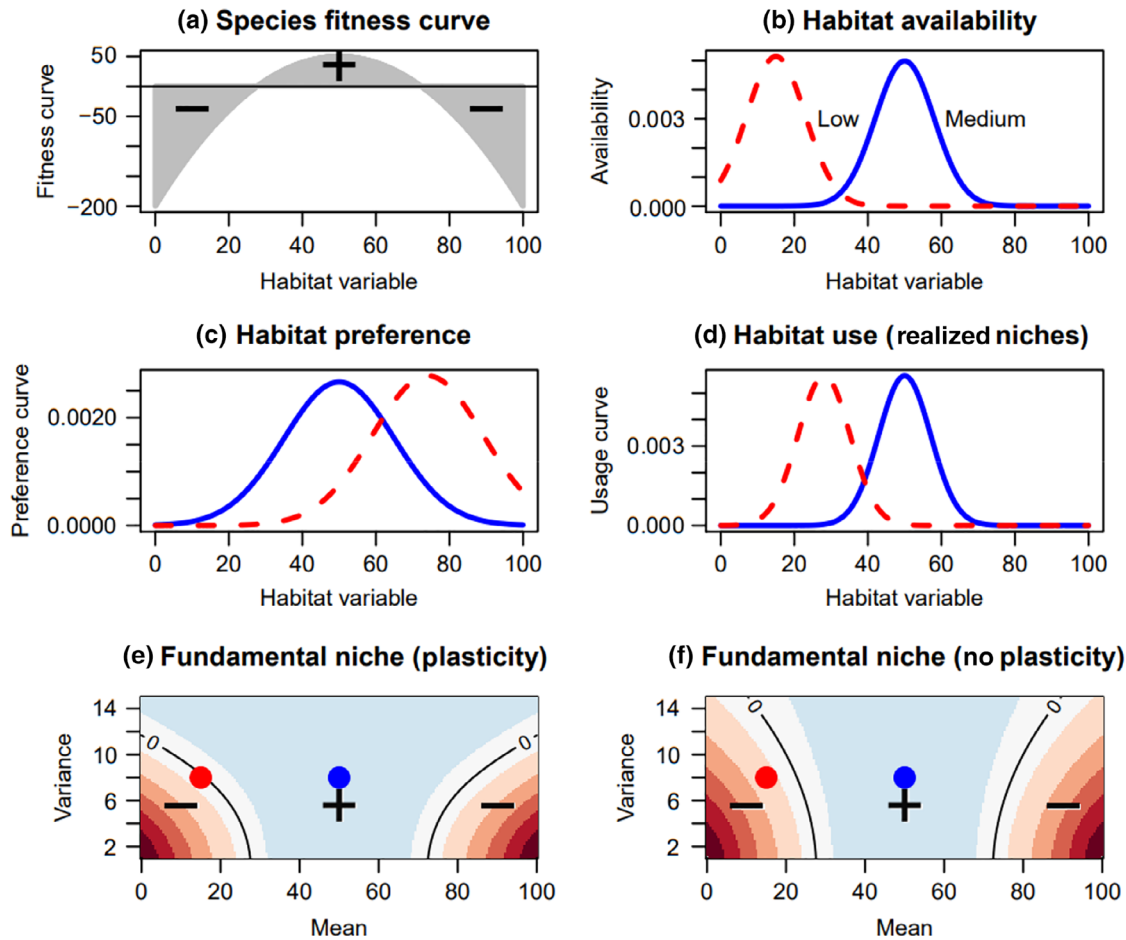


FIGURE 2 A simple example of how fitness, habitat availability, habitat preferences, and habitat use interact to shape the fundamental niche. (a) Fitness of the species for different values of the environmental variable. (b) Two profiles of habitat availability. The low- x scenario (dashed curve) represents a territory that has on average lower x values in comparison to the medium- x scenario (solid curve). (c) The corresponding habitat preference curves as might be inferred by fitting a habitat selection model to (d) the usage of points with different x values within the territory. (e) The two-dimensional niche space examines all possible combinations of mean and variance for the environmental profile of availability (hence each point in the space is a curve such as those shown in (b)). The blue and red dots correspond to the colored curves in the previous plots. The red color gradient indicates negative fitness and blue are positive. The white zones surround the boundary of the niche. (f) The consequences of removing behavioral plasticity from the animals so that their habitat preferences are invariant under habitat availability changes.

niche are given by solutions of the following equation in μ, σ :

$$\left(\frac{2\pi\sigma^2}{1-2\gamma_2\sigma^2}\right)^{\frac{1}{2}} \exp\left(\gamma_0 - \frac{\mu^2}{2\sigma^2} + \frac{(\gamma_1\sigma^2 + \mu)^2}{2\sigma^2(1-2\gamma_2\sigma^2)}\right) \times \left(\beta_0 + \beta_1 \frac{\gamma_1\sigma^2 + \mu}{1-2\gamma_2\sigma^2} + \beta_2 \frac{\sigma^2}{1-2\gamma_2\sigma^2} \left(1 + \frac{(\gamma_1\sigma^2 + \mu)^2}{\sigma^2(1-2\gamma_2\sigma^2)}\right)\right) = 0. \quad (24)$$

Removing the functional response from the model (by setting $\delta_{1,1} = 0, \delta_{2,1} = 0$), such that the animals have exactly the same habitat preference, regardless of habitat availability, gives rise to a different (smaller) niche (Figure 2f). Comparison of Figure 2e with 2f illustrates

the intuitive notion that in heterogeneous environments animals can improve their fitness by selectively using the better parts of their home range. As heterogeneity increases, it becomes more likely that animals can find and focus on extremely suitable places, extracting ever-higher fitness.

EXAMPLE 2: HOUSE SPARROWS IN SUBURBIA

I now apply these ideas to a real example based on the analysis of Matthiopoulos et al. (2019), which looked at fine-scale suburban garden composition within the home ranges of different sparrow colonies around Glasgow,

Scotland. The complete data set and analysis are included in the supplements to Matthiopoulos et al. (2019) (all niche-related figures below are produced as part of the Markdown pipeline based on these previous results and interested readers can experiment with the modeling decisions from the very start of the full analysis).

Home range composition was described in terms of six land cover variables. Sparrows were not particularly selective within their home ranges (the habitat preference model explained only 33% of observed patterns of usage), but the population models based on habitat availability and usage captured 81% of the variability in colony growth rates, under cross-validation, and were found to exceed the performance of models carrying no information on habitat heterogeneity. This high predictive ability was achievable with detailed information on the distribution of three of the six variables (grass, bush, and roof structures). Superabundance of any of these variables was detrimental to population growth. Sparrow colonies were least tolerant of high percentages of lawn and performed better in the presence of bushes and roof structures. Hence, although a full characterization of the fundamental niche of sparrows would require a more biologically sophisticated set of habitat variables, the suburban sparrow system is a good exemplar because it achieves high predictive power for a low number of niche dimensions and the simplicity of this example incurs no loss of generality for the mathematical framework. Indeed, the changes in the niche hypervolumes described below are likely to be more pronounced if more covariates were used.

An integral-free expression can be derived for suburban house sparrows, describing their fundamental niche's boundary in terms of garden composition (and heterogeneity therein), fitness parameters and habitat selection parameters. The habitat selection model fitted to the sparrow data in (Matthiopoulos et al., 2019) contained no quadratic terms in any of the habitat variables, which implies that $\gamma_{2,k} = 0$ and $\beta_{2,k} = 0$ for all k . This greatly simplifies Equations (22) and (23) to

$$\Theta_l = \prod_{k=1}^n \sqrt{2\pi}\sigma_k \exp\left(\gamma_{0,k} + \frac{1}{2}\gamma_{1,k}^2\sigma_k^2 + \gamma_{1,k}\mu_{l,k}\right) \quad (25)$$

$$Z_{0,k} = 1, Z_{1,k} = \gamma_{1,k}\sigma_k^2 + \mu_{l,k}. \quad (26)$$

The expression for $Z_{2,k}$ has been omitted since $\beta_{2,k} = 0$. Although this model was fitted to real scenarios from the field, and hence its parameters are data driven (Matthiopoulos et al., 2019), it can be used to quantify the niche in much simpler versions of environmental

space (e.g., unimodal availability clouds), revealing some highly informative features of the niche, under minimally realistic conditions.

To begin, let us assume for this illustration only, that sparrows occupy home ranges whose habitat composition can be described by a single (i.e., $L = 1$ and $\psi_1 = 1$) Gaussian component of n orthogonal variables (e.g., Jiménez et al. 2019). This means that habitat variables have unimodal, symmetric distributions within the home range and there are no correlations between them. To further reduce parameters, we will assume that the three environmental variables have the same dispersion. Hence, habitat availability $f_{\mathbf{x}} = \mathcal{N}_n(\mathbf{x}, \sigma\mathbf{I}_n)$ has spherical contours around a centroid $\mathbf{x} = (x_1, \dots, x_k, \dots, x_n)$ positioned at the average values of the three environmental variables (i.e., $x_k = \mu_k$). Here, σ is the standard deviation shared between the three environmental variables and \mathbf{I}_n is the $n \times n$ identity matrix. The parameter σ will be used here as a convenient shorthand for environmental heterogeneity. In particular, as $\sigma \rightarrow 0$, the entire home range comprises identical cells, each with composition \mathbf{x} . These simplifications of availability and E -space give a very tractable version of the niche boundary for sparrows

$$\prod_{k=1}^n \sqrt{2\pi}\sigma \exp\left(\gamma_{0,k} + \frac{1}{2}\gamma_{1,k}^2\sigma^2 + \gamma_{1,k}x_k\right) \times \sum_{k=1}^n (\beta_{0,k} + \beta_{1,k}\gamma_{1,k}\sigma^2 + \beta_{1,k}x_k) = 0.$$

Given that the first component of this product can never be zero, the expression further reduces to

$$\sum_{k=1}^n (\beta_{0,k} + \beta_{1,k}\gamma_{1,k}\sigma^2 + \beta_{1,k}x_k) = 0. \quad (27)$$

Under the GFR framework, the habitat selection coefficients can be written as functions of moments from the marginal distributions of the environmental variables (see Equation 17). In Matthiopoulos et al. (2019) these were sufficiently modeled as linear functions of the averages of all covariates, so that $\gamma_{1,k} = \delta_{1,k,0} + \sum_{i=1}^n \delta_{1,k,i}x_i$. This affords an expression for the niche in terms of purely $\beta, \sigma, \mathbf{x}$

$$\sum_{k=1}^n \left(\beta_{0,k} + \beta_{1,k}\sigma^2 \left(\delta_{1,k,0} + \sum_{i=1}^n \delta_{1,k,i}x_i \right) + \beta_{1,k}x_k \right) = 0.$$

Defining $\beta_0 = \sum_{k=1}^n \beta_{0,k}$

$$\beta_0 + \sum_{k=1}^n \left(\beta_{1,k} \sigma^2 \left(\delta_{1,k,0} + \sum_{i=1}^n \delta_{1,k,i} x_i \right) + \beta_{1,k} x_k \right) = 0. \quad (28)$$

For this example, it can be shown that the left-hand side of this equation is also equal to fitness, further facilitating interpretation. This expression was used to explore the fundamental niche of this population, within the much simplified, unimodal version of habitat availabilities in E -space. Below, I will refer to the average habitat composition $\mathbf{x} = (x_R, x_G, x_B)$ for roof, grass, and bush, as the “reference habitat,” a point in Hutchinsonian E -space. The only feasible reference habitats satisfy $x_R + x_G + x_B \leq 100\%$. Note that the three land cover variables were not exhaustive, because the habitat was characterized by other covariates for land cover. So, their sum could be any number between 0 and 1. I examined two scenarios of habitat composition. For the homogeneous scenario, I set $\sigma = 0$. For the heterogeneous scenario, the variability of habitats around the reference habitat $\mathbf{x} = (x_R, x_G, x_B)$ was explored by varying the value of σ from zero, up to its biologically feasible maximum. This was calculated in terms of the reference habitat \mathbf{x} via the following practical steps:

- In a heterogeneous home-range, different habitats $\mathbf{z} = (z_R, z_G, z_B)$ will be represented as points in E -space that are at some distance from the mean (i.e., the reference habitat \mathbf{x}).
 - Each of these points must satisfy positivity constraints and the 100% summation constraint ($z_R + z_G + z_B \leq 100\%$).
 - Gaussian densities $f_{\mathbf{x}}$ are, of course, unbounded so although they are mathematically convenient, some proportion of their density will “leak” outside feasible bounds, creating impossible habitats (i.e., negative proportions or total habitat proportions exceeding 100%).
 - The feasibility requirements will be more severely violated when σ increases to such an extent that a high proportion of probability density $f_{\mathbf{x}}$ is outside the 100% summation boundary.
 - To make sure that the results are not greatly affected by such violations and remain consistent across different reference habitats \mathbf{x} , I stipulated that home range heterogeneity (σ) would always retain >95% of the Gaussian density within the feasible region.
 - I defined the radius r of a sphere in E -space around the reference habitat, as the 95th percentile of the Gaussian density $f_{\mathbf{x}}$. For a variate with a multivariate standard normal $\mathcal{N}_3(\mathbf{0}, I_3)$ distribution, the square of the Mahalanobis distance is chi-square distributed, with critical value at 95% of $\chi_3^2(1 - 0.95) = 7.815$. So, the critical distance is $r = \sigma \sqrt{7.815}$.
- The maximum value that this could take is $r_{\max} = \min(x_R, x_G, x_B, d)$, where $d = (1 - x_R - x_G - x_B) / \sqrt{3}$ is the distance of the reference habitat \mathbf{x} from the inclined plane of 100% land cover.
 - This implies that the maximum value σ_{\max} of the heterogeneity parameter σ is $\sigma_{\max}(\mathbf{x}) = r_{\max} / \sqrt{7.815}$.

Within the feasible interval $\sigma \in [0, \sigma_{\max}(\mathbf{x})]$, I defined viability as the occurrence of a positive value on the left-hand side of Equation (28). I also recorded these values as the measure of fitness at each reference habitat \mathbf{x} . For the homogeneous scenario, only one value of viability and fitness corresponded to each reference habitat. For the heterogeneous scenario, I recorded the maximum achievable fitness and the corresponding value of habitat heterogeneity σ that produced it.

I generated the following statistics to examine the impact of heterogeneity and habitat selectivity on the niche. First, the percentage of feasible environmental space that contained viable reference habitats for the homogeneous case. Second, the percentage of reference habitats whose fitness was improved with the addition of heterogeneity and selectivity. Third, the percentage of inviable reference habitats that were made viable with the addition of heterogeneity and selectivity. Fourth, the percentage of increase in fitness resulting from the addition of heterogeneity and selectivity.

Under the assumption of home range homogeneity (i.e., under the Hutchinsonian n -hypervolume definition of the fundamental niche), I found that the niche occupied 15% of feasible E -space (Figure 3a). Introducing habitat heterogeneity and sparrow selectivity allowed an increase of the complete set of habitats that could be included in viable home ranges to 25% of feasible space (Figure 3b). Improvements in the maximum fitness of animals encountered in different habitats, occurred primarily in the center of viable space (Figure 3c) because this form of spherical heterogeneity could not be high close to the borders of the feasible niche space, where $\sigma_{\max} \rightarrow 0$. The fitness characterizing entire home ranges was also improved compared to the homogeneous scenario (Figure 3d), because sparrows could select to use the better-than-average parts of their heterogeneous home ranges. In 9% of previously viable homogeneous home ranges, fitness was improved when habitat heterogeneity and selectivity were introduced and an additional 0.15% of previously inviable ranges became viable (essentially, this represents the scenario where the mean values of habitat variables imply extinction, but the species can survive by using small refuge parts in their home range selectively). The average improvement in fitness was 13.28% (95% CI: 0.03%, 80.99%). It is notable that these

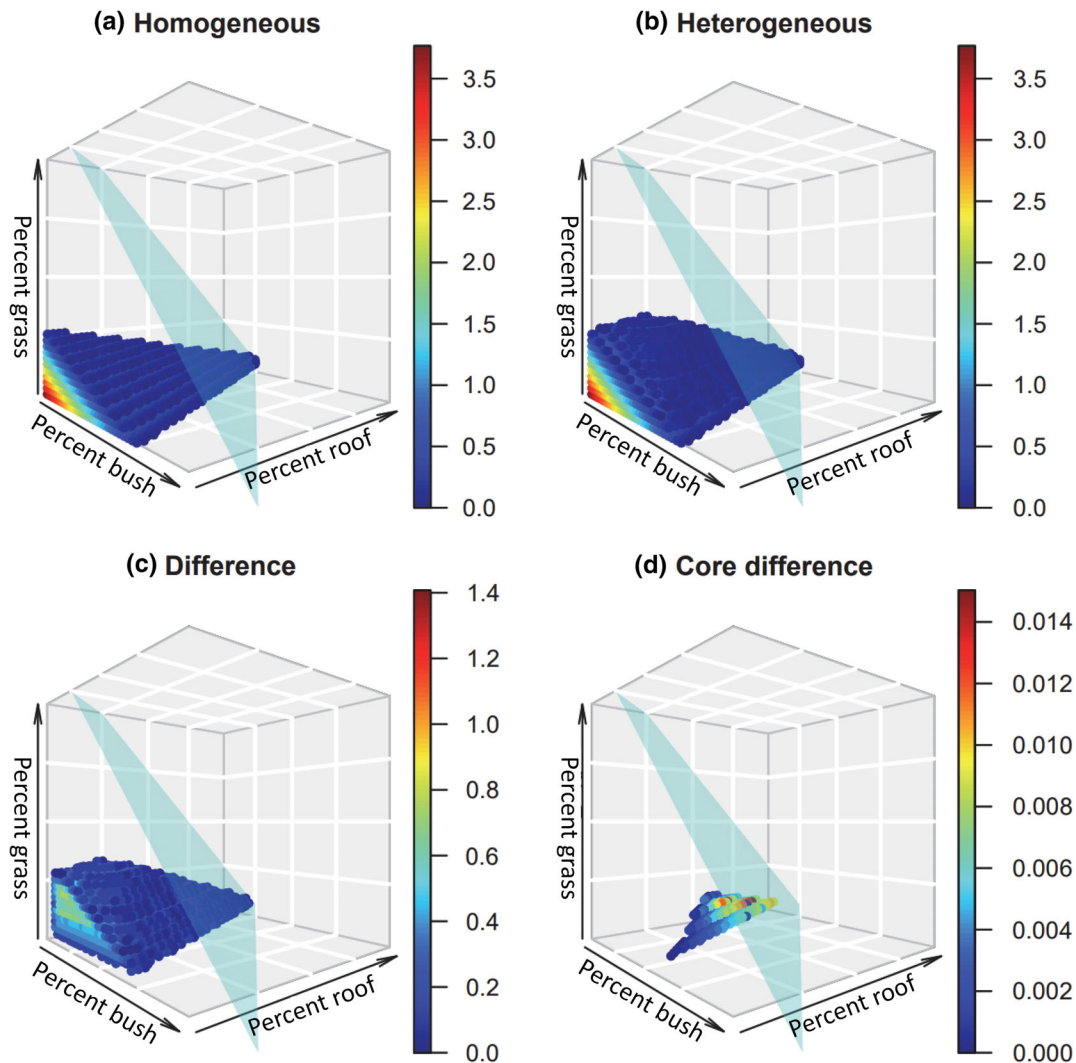


FIGURE 3 Visualizing the fundamental niche of house sparrows in homogeneous and heterogeneous home ranges. The transparent plane represents a feasibility boundary, preventing the sum of the three land cover variables from exceeding 100%. The three axes are plotted from 0% to 80%, to better focus on the viable region. Relative fitness values (or their differences) are colored on a gradient from high (red) to low (blue). The homogeneous scenario (a) assumes that all parts of a home range have the same composition as the average of the home range: the reference habitat. Hence, (a) is a data-derived representation of Hutchinson’s *E*-space hypervolume for the sparrows in this study. The heterogeneous scenario (b) encloses all habitats that occur in viable home ranges when the heterogeneity in a home range maximizes fitness. The difference (c) between the predictions of the two scenarios highlights which regions of the homogeneous fundamental niche benefit from the existence of habitat heterogeneity and sparrow selectivity. The core difference (d) compares the change in relative fitness for homogeneous and heterogeneous home ranges with the same average habitat composition.

levels of niche and viability inflation are observed in a model with only three environmental covariates, under the most rudimentary form of heterogeneity (i.e., a shared variance parameter for all environmental variables, with no multimodality or asymmetries) and in a study species that demonstrated limited selectivity for habitats within the individual colony range. This is therefore a stringent demonstration, using field data, of the original hypothesis that heterogeneity and behavioral plasticity alter the shape of Hutchinson’s fundamental niche in a real species.

NECESSARY ADJUSTMENTS TO OUR NOTION OF THE FUNDAMENTAL NICHE OF ANIMALS

The fundamental niche began life a century ago (Grinnell, 1917), as an aid to scientific intuition (Parentoni Martins, 2017). However, as our broader ecological understanding has developed, we have unveiled many of the limitations of our textbook schematics of the niche (Angilletta et al., 2019; Araújo & Guisan, 2006).

At the same time, the proliferation of niche-related models in the management of vital ecosystems, means that our intuition about the niche is more important and relevant than ever (Holt, 2009; Hurlbert, 1981). By formulating models of the fundamental niche appropriate for vagile and selective animals in heterogeneous environments, the above synthesis has brought the following conceptual adjustments into sharper focus.

It has more dimensions than Hutchinson's niche space

The environments experienced by animals cannot be characterized sufficiently as single points in E -space, as Hutchinson had envisaged. Habitat availability clouds in environmental spaces may have multiple loci, they are not necessarily convex and may often have discontinuities or holes (Blonder, 2016, 2018; Jimenez & Soberón, 2021; Soberón & Peterson, 2020). Animals respond selectively to these complex availability clouds and their fitness is determined by the *entirety* of these interactions. The two examples in this monograph, as well as the extensive theoretical spatial literature (Tilman & Kareiva, 1997), have shown that spatial heterogeneity matters for fitness. Therefore, the didactic “severing” (Colwell & Rangel, 2009) between E - and G -spaces that served Hutchinson so well, now needs to be reconsidered. Spatial heterogeneity leads to variance, autocorrelation, and multimodality in availability clouds. Representing these important statistical properties in niche spaces requires the introduction of additional degrees of freedom, more niche dimensions (Hurlbert, 1981).

For instance, in the sparrow example above, only three environmental variables were considered, but to fit the model to real data, a total of 57 dimensions were used to describe the heterogeneity in garden compositions. Such high dimensions are evidently required by the data because they persist through various filters of model parsimony (e.g., model selection, regularization, cross-validation). To illustrate the predictions of such high-dimensional models in three-dimensional Hutchinsonian E -space (Figure 3), I specified the fully fitted model to the simplest scenario of habitat heterogeneity, using unimodal Gaussian spheres in E -space. This meant that the niche model was explored in four-dimensional space (i.e., the three mean values for the land cover variables with the addition of a common variance dimension describing habitat heterogeneity within a home range). The extent and consequences of this rudimentary form of heterogeneity in the sparrows' home ranges could then be examined by increasing a single variability parameter σ from zero (i.e., homogeneous home range), to its largest feasible value. The visualizations in Figure 3, therefore, represent the minimum

deviation from Hutchinson's niche space because they use only one more dimension (the variance) than the three environmental variables in the system. The resulting inflation in the fundamental niche indicates that these increases in dimensionality are not just theoretically but also quantitatively influential. Importantly, such high-dimensional niches have been explicitly anticipated, as a reconciling route between the predictions of niche and neutral theories (Clark et al., 2007).

Using more degrees of freedom to describe more complex environmental objects is an obvious (Hurlbert, 1981), but somewhat daunting (MacNab, 2018), solution to dealing with the diversity of habitats experienced by individual animals. However, the “curse of dimensionality” (Bellman, 1957) is not a mathematical problem, it is primarily a statistical one. As the number of dimensions increases, optimization or Monte Carlo Markov Chain algorithms need more iterations to estimate relevant parameters, and the volumes of parameter space that can be informed by available data become sparse. The theoretical framework presented here and elsewhere (Matthiopoulos et al., 2015), demonstrates that high-dimensional calculations with the fundamental niche can be approached analytically, reducing the model-fitting component to the form of generalized linear models (see application in Matthiopoulos et al., 2019), a type of inferential tool that can deal efficiently with many hundreds of dimensions. Further, as I argue below (*The multiplicity of realized niches is a blessing, not a curse and Future developments: Data requirements and statistical inference*), the issues of data sufficiency can be identified and addressed via data integration of multiple instances and types of data.

It is not necessarily a bounded subset of E -space

Hutchinsonian niches focus on environmental conditions (e.g., temperature, humidity, etc., often called “scenopoetic” variables; Colwell & Rangel, 2009; Hutchinson, 1978; Soberón & Nakamura, 2009), characteristics that set limits to viability (Godsoe et al., 2017). As a result, fundamental niches are often defined as hypervolumes with a well-defined core, suspended in E -space (Blonder et al., 2014; Soberón & Peterson, 2020). Applied work has adhered to this image, by often focusing on niches of finite volume and breadth (e.g., Broennimann et al., 2012, Carscadden et al., 2020 and, also, the sparrow example above).

However, Hutchinson recognized that resources also have a role to play in defining niche spaces (Colwell & Rangel, 2009; Hurlbert, 1981; Kearney et al., 2010). Unlike fitness responses to conditions (which usually correspond to maximum and minimum tolerances), fitness responses to

resources are unbounded (i.e., organisms are not likely to die if they are surrounded by too much food, unless this is at the expense of other valuable resources). Other authors have noted the importance of (real, or perceived) risk in shaping species distributions (DeCesare et al., 2014). Responses to risks are only bounded below by zero (i.e., everything else being equal, the lower the risk, the better).

The inclusion of resources and risks (collectively known as “bionomic” variables; Colwell & Rangel, 2009; Hutchinson, 1978; Soberón & Nakamura, 2009) into the definition of *E*-space was considered challenging because they tend to interact dynamically with the species of interest (see considerations of multispecies interactions in *Future developments: Mechanistic content of models leading to the niche*). However, from a biological perspective, resources and risks are prominent in determining the ability of a species to survive and hence our intuitive image needs to be adjusted to admit niches that are unbounded above (along resource axes) or are in contact with zero (along risk axes).

It is more malleable, but also more predictable

A corollary of the high dimensionality of animal niches is that niche boundaries in *E*-space may appear less predictable (“fuzzy”; Angilletta et al., 2019) than they are. Certainly, process stochasticity, individual variation and observation errors will make the niche boundaries nondeterministic, but some of their apparent uncertainty may be due to our misrepresenting them as lower-dimensional objects. This implies that the fundamental niches of animals are more malleable than has thus far been imagined. Heterogeneous environments can be more favorable to a mobile and selective species than homogeneous ones (even ones that are “on average” marginally better). Even environments that are hostile on average can offer localized refugia and therefore encourage species viability (Pettersson & Nilsson Jacobi, 2021). The framework presented here can quantify exactly how buffered real animals are from hostile environments.

It is worth asking, whether the flexibility of the niche in these extra dimensions is enough to have an impact on population ranges and extinction probabilities. The sparrow example above indicates that it is, by demonstrating measurable impacts on the volume of the niche, under even the slightest deviations from Hutchinson’s definition of dimensionality. Given that the framework presented here for the estimation of fundamental niches is very new, it is not yet clear what proportion of the apparent uncertainty characterizing these estimates in real systems will be due to dimensionality versus sources of noise. However, it is possible that if we model the

niche in its full complexity, it may prove to be more deterministic (hence, predictable) than we might conclude by working purely with its low-dimensional projections, a situation echoed in other areas of dynamical systems science (Farmer et al., 1983).

The multiplicity of realized niches is a blessing, not a curse

It is true that the fundamental niche of a species cannot be estimated from a single snapshot of its population distribution, i.e., from a single realized niche (Angilletta et al., 2019; McInerney & Etienne, 2012a). It is also true that the uncritical pooling of spatial data will lead to biased representations of the niche (Colwell & Rangel, 2009; Godsoe, 2010; Jiménez-Valverde et al., 2008; Peterson et al., 2011; Pulliam, 2000; Soberón & Peterson, 2005). However, multiple realized niches, when treated as sampling instances in formal statistical estimation, allow the partly obscured picture of the fundamental niche to be assembled from different viewpoints. This process of reconstructing a latent object from its partial reflections is no different to any other estimation problem in the sciences (see discussion in Godsoe, 2010).

The above synthesis shows how to formulate the fundamental niche mathematically in a way that allows its empirical estimation from distributional and population growth data collected in multiple realized niches. The key to achieving this is to treat the multiplicity of realized niches as an inferential strength, rather than a nuisance. In this way, the niche object, estimated from case studies such as the sparrow example, is an approximation of the species’ fundamental niche that will asymptotically improve as more (contemporary and historical) data from the worldwide range of a species are included in the modeling. The rate at which this approximation converges with diverse data, for different taxa, is an important future research question. It might be argued that presence-only models of the niche (e.g., Broennimann et al., 2012; Drake et al., 2006; Hirzel & Arlettaz, 2003; Rotenberry et al., 2006; Thuiller et al., 2004) share such an asymptotic convergence to the fundamental niche because as ever-more presence-only data are pooled into these analyses, we map out more of the niche space. However, there are some critical statistical requirements that are not satisfied by presence-only models. The above synthesis of the extensive niche literature hints at four such key requirements, that should be met in any future statistical model of the fundamental niche:

1. Combination of spatial distribution *and* population growth or demographic data, ideally as part of simultaneous model fitting;

2. Integration of data from multiple instances, across a wide range of habitat availability and population density scenarios, that acknowledge the availability composition of each scenario and the possible imbalances in sample size between scenarios;
3. Accounting for density-dependent effects (on both population growth and distribution) at the model fitting stage, even if the subsequent calculation of the niche is done by setting population densities close to zero;
4. Separation of the habitat fitness and habitat selection coefficients (i.e., the distinction between the betas in Equation 9 and the g in Equation 15). This current confounding between fitness and selection in our niche-related models is a source of much confusion and prediction bias.

These principles are also direct consequences of the dominant formalization of niche theory, the BAM diagram of Soberón and Peterson (2005) and Soberón (2007). They refer mostly to how we capitalize on our existing species distribution data and models, that have served as the bedrock for the ideas in this paper and most niche-related empirical models. However, the approach is not incompatible with other sources of information about the fundamental niche. It has previously been argued (e.g., Jiménez et al., 2019) that estimation of fundamental niches can only be approached by models of biophysical first principles (e.g., Kearney & Porter, 2004) or via experimental methods (e.g., Colwell & Fuentes, 1975). The multiplicity of realized niches offers us a third route to statistical estimation of the fundamental niche, that is entirely complementary to the information contained in first principles and experimental data. For example, experimental data on species distributions may be equivalent to sampling instances whose habitat availabilities are controlled or simplified (e.g., by creating homogeneity in habitats along one or more dimensions of niche space). Such experimental data could be analyzed together with field data, offering important anchor points for the model to tie onto. Mechanistic principles are an even more fruitful source of biological realism, so I will discuss them below as an important extension to the present framework (see *Future developments: Mechanistic content of models leading to the niche*).

The only thing constant is change, but not all change should affect the fundamental niche

One of the key assumptions of models for the fundamental niche is that it is a stationary characteristic of a species (Holt, 2009; Nogués-Bravo, 2009; Pearman et al., 2008). We often imagine that the same fundamental, unchanging

rules, merely express themselves differently in different environments, presenting us with different realized niches. This stationarity assumption is convenient, because it allows us to extend the predictive reach of our models into new environments, but it is rarely true (Cassini, 2011). It is therefore important to identify the different sources of change in ecosystems and to consider how they might relate to the validity of the stationary niche ideal.

First, there is environmental change, resulting either from temporal trends, or from looking at a species at different places, with different habitat availability profiles. The statistical approach discussed throughout this monograph, and the distilled principles of niche-related inference discussed in *The multiplicity of realized niches is a blessing, not a curse*, are designed to ensure that the estimated parameters of fitness (and the subsequent estimates of the niche) are unaffected by such changes.

Second, there are intrinsic sources of change, due to population dynamics. It makes biological sense that the fitness of individuals and their use of habitats will be affected by population density (Boyce et al., 2016; Cassini, 2011; Fretwell & Lucas, 1969; McLoughlin et al., 2010; Rosenzweig, 1991). Indeed, taking population dynamics into consideration has been shown to improve the predictions of species distribution models (Matthiopoulos et al., 2015; Pagel & Schurr, 2011), and, once again, the fitness parameters in the framework developed here are designed to be invariant under population change.

Ostensibly, a rather difficult situation occurs when both density and the environment are changing. This scenario coincides with one of the preeminent areas of application of SDMs, in invasive species and, more generally, in range dynamics (Allouche et al., 2008; Gallien et al., 2010; Hargreaves et al., 2014; Pagel & Schurr, 2011; Schurr et al., 2012), when zones in the range of a species are experiencing new habitat compositions at the same time as undergoing transient population dynamics. Once again, a niche model that accounts for multiple environments and gradations in density can deal with both these problems simultaneously. Related to range dynamics is the broader problem of dispersal effects on niche models. An unsuitable region (sink) may keep getting colonized by nearby thriving populations (sources) and, counterintuitively, under certain scenarios of connectivity, sinks may appear to be more densely populated than sources (Hanski & Gilpin, 1997). Conversely, a suitable region may be as-yet uncolonized because there are no nearby sources. These consequences of dynamic dispersal processes can confuse our models of fundamental niche (Pulliam, 2000), but rather than allowing them to affect the estimates of the niche, we must allow our models to incorporate the spatial context of transient dispersal processes (Schurr et al., 2012).

The third source of change comes from dynamic interactions with resources or other species in the ecosystem. Depletion and multispecies dynamics are rarely considered in fundamental niche models, despite the recognition of their importance (Godsoe & Harmon, 2012) and the fact that the alternative concepts of Eltonian and Grinnellian niches place the emphasis firmly on community interactions (Soberón, 2007). This unification of the niche concepts is currently at the frontier of ecological research (see *Future developments: Mechanistic content of models leading to the niche*).

The fourth source of change is evolution (Godsoe et al., 2022). Over sufficiently long time periods, populations will change, causing their fundamental niche to drift (Pearman et al., 2008). The volatility in the evolutionary dynamics of the fundamental niche may not be matched by the dynamics in realized niches (Colwell & Rangel, 2009). Measures of genetic dissimilarity between subpopulations, as well as measures of within-population individual variation will become particularly valuable when trying to apportion changing distributions to environmental versus evolutionary change. Longer-term, there might be scope for modeling the feedback loops between the habitats that organisms are exposed to today and the habitats that they will intrinsically find suitable tomorrow, as a result of adaptation (see *Future developments: Mechanistic content of models leading to the niche*).

Explaining all the variation we see between realized niches as the result of changes in the fundamental niche is clearly undesirable. For the sake of transferability (Yates et al., 2018), the key practical contribution of the fundamental niche will be to quantify the invariant core of a species, at least, at some point of its evolution. In this section, I have argued that, under the present framework, at least two sources of change (environmental and population dynamics) will leave the estimates of the niche unaffected. The other two sources (community and evolutionary dynamics) still need to be controlled for, by extending the framework. These, and other future extensions are considered next.

FUTURE DEVELOPMENTS

The semantics of niche theory challenge our ecological intuition (Warren, 2013) and we still have some way to go in incorporating key biological features, such as dispersal limitation, evolutionary insights, and transferable, quantitative predictions for the composition of real communities (Chase, 2016). However, the foundations reviewed and synthesized in this monograph are solid, and developments need to happen in the three crucial areas of mechanistic modeling, statistical inference and ecological application.

Mechanistic content of models leading to the niche

Mismatches between our estimates of the fundamental niche and empirical species distributions are likely to be caused by the omission of biological mechanisms relating to physiology, behavior, density dependence, dispersal, individual variation, and multispecies interactions (Hargreaves et al., 2014; Pulliam, 2000).

Physiological constants, metabolic conversion efficiencies, allometric scalars and conservation of mass/energy principles can all be used to constrain the parameters and functional form of niche models (Kearney et al., 2008, 2010; Kearney & Porter, 2004). Furthermore, interactions between resources in how they impact the fitness of a species can benefit from the extensive literature on complementarity and substitutability (Tilman, 1980).

Behavioral patterns in selectivity and movement are captured, to an extent, by the incorporation of mobility and habitat selection in the framework presented here. However, long-range regular migrations or complex accessibility constraints such as those caused by sea currents/wind fields (Weimerskirch et al., 2012) or landscape resistance mechanisms (Beyer et al., 2016) could still bias the niche parameter estimates.

Density dependence originating from crowding is captured by the present framework (Matthiopoulos et al., 2015) by incorporating attrition onto fitness as a result of conspecific density. However, Allee effects (Courchamp et al., 1999) at low densities are not, and these remain an important future addition (Holt, 2009; Holt et al., 2004).

Dispersal processes are relevant because of two key assumptions about the niche (used in *Population dynamics in E-space*). First, the fundamental niche must contain environments of nonnegative population growth, irrespective of whether these environments are accessible via dispersal from the species' current range (e.g., as identified in the BAM diagram of Soberón and Peterson, 2005; Soberón, 2010). Second, the niche must exclude instances of apparently positive population growth achieved via supplements from source habitats (Pulliam, 2000). Real populations from which our data are likely to originate are affected by these transient or permanent complications relating to dispersal. Therefore, proximity to donor populations, at distances larger than the typical home-ranging movement of individuals needs to inform the existence and growth rate of focal populations. In addition, particular species will have different patterns of mobility and these may vary during different life-stages or seasons. For example, some colonial species such as seabirds, might behave as nomads, during their juvenile years, as central-place foragers during their provisioning stages and as long-range migrants, outside of

their breeding season. Extending the present framework to include such complexities, into a more holistic definition of fitness, is a key priority for future work.

A further important extension of the present framework would be the inclusion of individual variation (Angilletta et al., 2019). Much of the material presented here was developed for populations or species but has continuously referred to the mobility and behavior of “typical” individuals (Holt, 2009). Therefore, any predictions from these models do not capture potential phenotypic variation that could, in principle, characterize each individual by its own, fundamental niche. This hierarchy of fundamental niches (Holt, 2009), from individuals (Carlson et al., 2021), to populations, to entire species has important implications for our understanding of evolutionary processes (Carscadden et al., 2020) in dynamic landscapes. Versions of the framework presented here, extended to include individual variation, are entirely feasible, given the computational efficiency of the calculations involved and a good understanding of evolutionary processes at the level of species–habitat associations can only benefit from knowledge of the shape and properties of the fundamental niche (Soberón & Peterson, 2020).

Increasing the mechanistic content of the models presented here could also deal with a closely related limitation of Hutchinson’s fundamental niche (McInerney & Etienne, 2012b), its apparent inability to capture interspecific interactions such as predation, mutualism or competition. Perhaps the boldest simplification of Hutchinson’s theory of fundamental niches was to ignore multispecies interactions (occasionally distinguishing between pre-interaction and post-interaction niches; Colwell & Rangel, 2009). Certainly, examining species in isolation is a valid starting point for developing theory (Roughgarden, 1974), but the fall from grace of niche concepts from the 1980s onward (Colwell & Rangel, 2009; Sales et al., 2021) was associated with the realization of the importance of species interactions (Rosenzweig, 1991; Rosenzweig & Abramsky, 1985) in shaping population sizes and distributions (Colwell & Rangel, 2009).

These considerations require us to think of the niche in more dynamic terms (Chase & Leibold, 2003; Parentoni Martins, 2017; Schurr et al., 2012; Soberón, 2014), driven by biotic, and not just scenopoetic, variables. Potentially, we may arrive at a mathematical formulation that hybridizes the Grinnellian & Eltonian ideas of the niche as a *role in the ecological community* with the Hutchinsonian idea of the niche as a *volume in E-space* (Chase & Leibold, 2003; McInerney & Etienne, 2012b; Peterson et al., 2011).

Such a formulation would capture dynamical interactions by including other species (prey, predators, competitors) as additional dimensions of *E-space* (Godsoe et al., 2017; Pulliam, 2000; Whittaker et al., 1973), an idea

that may not have universal appeal because it integrates the niche with its community context. However, as shown here, it is both possible and necessary to formulate the fundamental niche in a context-dependent way, as long as the space of possibilities is sufficiently high dimensional to capture all possible contexts. Indeed, the idea of simultaneous modeling of the niches and distributions of multiple interacting species is already two decades old (Guisan & Zimmermann, 2000) and rapidly gaining momentum (Godsoe et al., 2017; Kissling et al., 2012; Ovaskainen & Abrego, 2020). These emerging and exciting multivariate frameworks already have at their core a working definition of the niche, which has yet to satisfy the stationarity properties of the fundamental niche (see *Necessary adjustments...: The only thing constant is change...*). The work presented here can move that definition more towards the assumption of stationarity.

Data requirements and statistical inference

The synthesis presented here attempts to bridge the gap between fitness models and distribution data. This convergence between mechanism and inference requires us to ask how feasible the data requirements are, how achievable the model fitting is, and how it can attain precision and minimize bias. I consider these questions in turn.

On the question of data requirements, the proposed approach (and, in particular, the separation of fitness parameters from distribution parameters, the increase in the dimensionality of the niche space, and the acknowledgment of functional responses in habitat selection) causes a necessary increase in the number of parameters required by the fundamental niche model compared to a typical SDM. The general rules for data adequacy are to obtain (1) species distribution data from multiple, diverse environmental scenarios where (2) the environmental variables are known at a resolution relevant to the behavioral process of selection by the study animals and where (3) for some of these sampling instances there are accompanying data on population growth. These are not difficult requirements for a great many species. For instance, for the sparrow example in *Example 2: House sparrows in suburbia*, a postgraduate student collected in situ observations of sparrow usage, during a summer project, from 1280 distinct spatial locations within suburban gardens and matched those to garden composition using Google Earth imagery. A total of 32 sparrow colonies were included in the study. For 12 focal sparrow colonies, baseline population surveys were available from a citizen

science program, the Glasgow House Sparrow Project, part of a partnership between the Royal Society for the Protection of Birds (RSPB) and the University of Glasgow. The explanatory and predictive power of the model fitted to these data were characteristically high (Matthiopoulos et al., 2019) despite the modest data collection effort.

On the question of fitting methods for incrementally mechanistic models. Current mechanistic approaches propose to build fundamental niches from the ground up, using only biological first principles. The advantage of mechanistic models is in their ability to define the qualitative, quantitative, and interactional relationship between fitness and the environmental variables (Kearney et al., 2010). Mechanistic principles transcend the range of observed environments and realized niches, so they promise to increase the transferability of niche models (Bolker, 2008; Mouquet et al., 2015; Yates et al., 2018). On the other hand, the emphasis on mechanism faces the challenges of reductionism (Holt, 2009; McInerney & Etienne, 2012a; Peterson et al., 2015; Schurr et al., 2012) and currently seems restricted to capturing well-understood and univariate physiological tolerances (e.g., thermal envelopes).

Nevertheless, statistical analyses of the niche cannot go far without biological mechanism (McInerney & Etienne, 2012a). For example, above, I have argued that spatial data cannot estimate the niche without information on population growth, density dependence, and demography (Aldridge & Boyce, 2008; DeCesare et al., 2014; Matthiopoulos et al., 2015; Pagel & Schurr, 2011; Schurr et al., 2012). Equally, it seems foolhardy to attempt predictions of species realized niches, based purely on mechanistic models, without fitting them to distribution data (Peterson et al., 2015). Therefore, a reconciliation between mechanistic and correlational models is necessary.

Although, the distinction between these two types of models is made quite often in the modern niche literature (Gallien et al., 2010; Kearney et al., 2010; Kearney & Porter, 2009; Peterson et al., 2015; Yates et al., 2018) the separation is not unequivocal. In reality, no model is purely mechanistic and almost every model (apart from the simplest forms of statistical regression) will be a hybrid of some sort. I outline here four routes to increasing the mechanistic content of niche models while retaining their link to SDMs.

First, many mechanistic principles can be satisfied using very rudimentary mathematical forms that are regularly used by most correlational models. Within a linear predictor (e.g., Equation 9 above), monotonic forms can describe risks and resources, quadratic forms can describe conditions, and interactions can describe substitutable,

antagonistic, and complementary environmental variables (chapter 2, in Matthiopoulos, Fieberg, Aarts, 2020). It may therefore be that even the existing correlational models described in this paper offer us considerable mechanistic control.

Second, extending correlational models to afford more user control regarding parameters (e.g., by using informative priors in a Bayesian setting, or constrained regression in a likelihood setting) would allow the incorporation of known biological first principles and quantitative knowledge on fitness–covariate relations and interactive effects (Jiménez et al., 2019).

Third, when more complicated relationships are involved so that environmental covariates have cumulative, delayed, or saturating effects on species fitness and distribution (Kearney et al., 2010), the use of mechanistic models may inform us about appropriate nonlinear empirical functions that can be used to approximate the behavior of mechanisms.

Fourth, when existing or approximate mathematical models cannot be used, it is increasingly possible to fit mechanistic models directly to data (Mouquet et al., 2015).

Such flexible modeling approaches also bear relevance to the question of precision. As we move towards the use of integrated modeling in ecology (Kindsvater et al., 2018; Yen et al., 2019), it becomes possible and valuable to draw joint inferences from spatial and population data. Simultaneous model fitting to these different data types permits information to flow in both directions (i.e., from the species distribution model to the population model and vice versa) and it also allows the correct propagation of errors through the different stages of analysis. Hence, acknowledging the correlations between parameters in the model can avoid the unnecessary compounding of errors at the cost of estimation and prediction precision.

On the question of bias. Although the definition of the fundamental niche considers small and isolated populations of identical individuals that are unaffected by interactions with other species, the data on which these models are fitted are almost certain to be affected by these processes. When this happens, the parameters of the niche model will suffer from bias. So, the recognition and gradual incorporation of the mechanisms described in *Mechanistic content of models leading to the niche* is a necessary route to progress.

Optimizing ecosystem management

Niches that exist in tens or hundreds of dimensions are hard to visualize, but having a compact and numerically efficient expression that describes the boundary of the niche is arguably more useful than visualizing it, because it allows us to

identify viable environments (Godsoe, 2010) and to manage land cover so as to optimize population viability. By subtly modulating the availability and heterogeneity of environmental variables, this framework allows us to engineer viability for a species where there previously may have been none (Fig 4. in Matthiopoulos et al., 2019). As Figure 1 illustrates, we can do this without necessarily changing the overall proportions of habitats in a landscape, by merely rearranging them spatially. The vast body of literature on metapopulations and habitat fragmentation (Hanski & Gilpin, 1997) bears witness to this principle. Given the reality of conflicts between conservation, resource/pest management, wealth creation, food security, and complex ecosystem dynamics, where the overall amounts of land cover for each activity are often fixed (Phalan et al., 2011), achieving such accurate mitigation via landscape management (Sayer et al., 2013) will prove invaluable in the future. We are in a good position to achieve this, because ecological thinking and computer algorithms on spatial prioritization have been advancing for decades (Moilanen et al., 2008). Niche theory now needs to provide that research community with objective functions for fitness, habitat suitability and critical habitats.

CONCLUSION

As ecology is moving towards transferable models of population viability and distribution (Araújo & Guisan, 2006; Leibold, 2008; Yates et al., 2018), the fundamental niche is an indispensable concept (Soberón, 2014; Warren, 2012). The niche must be pattern and data driven (Schurr et al., 2012; Warren, 2012), but it must be rooted in ecological principles and applied imperatives (McInerny & Etienne, 2012c). I have argued for the use of hybrid (McInerny & Etienne, 2012b) correlational-mechanistic approaches (Kearney & Porter, 2004; Schurr et al., 2012), that bring to the fore issues of population growth, transient dynamics, resource depletion and interspecific interactions. Taking environmental heterogeneity and phenotypic plasticity (Angilletta et al., 2019) into account has led to a reevaluation of the complexity of the fundamental niche, a route towards its evolution as a concept, rather than its abandonment. My early results on the malleability of Hutchinson's fundamental niche carry optimistic messages about the resilience of animal species to anthropogenic change and the available room for maneuver in mitigating human-wildlife conflicts.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are published as supporting information to Matthiopoulos et al. (2019) at <https://royalsocietypublishing.org/doi/suppl/10.1098/rspb.2018.2911>. Code (JasonMat, 2022) is provided in Zenodo at <https://doi.org/10.5281/zenodo.6609762>.

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REFERENCES

- Aarts, G., J. Fieberg, S. Brasseur, and J. Matthiopoulos. 2013. "Quantifying the Effect of Habitat Availability on Species Distributions." *Journal of Animal Ecology* 82: 1135–45.
- Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. "Estimating Space-Use and Habitat Preference from Wildlife Telemetry Data." *Ecography* 31: 140–60.
- Aldossari, S., D. Husmeier, and J. Matthiopoulos. 2021. "Generalized Functional Responses in Habitat Selection Fitted by Decision Trees and Random Forests." Proceedings of the 3rd International Conference on Statistics: Theory and Applications (ICSTA'21): 2–5.
- Aldridge, C. L., and M. S. Boyce. 2008. "Accounting for Fitness: Combining Survival and Selection when Assessing Wildlife-Habitat Relationships." *Israel Journal of Ecology & Evolution* 54: 389–419.
- Allouche, O., O. Steinitz, D. Rotem, A. Rosenfeld, and R. Kadmon. 2008. "Incorporating Distance Constraints into Species Distribution Models." *Journal of Applied Ecology* 45: 599–609.
- Angilletta, M. J., M. W. Sears, O. Levy, J. P. Youngblood, and J. M. VandenBrooks. 2019. "Fundamental Flaws with the Fundamental Niche." *Integrative and Comparative Biology* 59: 1038–48.
- Araújo, M. B., and A. Guisan. 2006. "Five (or So) Challenges for Species Distribution Modelling." *Journal of Biogeography* 33: 1677–88.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, W. Gerald, S. Ecology, N. Jan, S. M. Arthur, B. F. J. Manly, and G. W. Garner. 1996. "Assessing Habitat Selection when Availability Changes." *Ecology* 77: 215–27.
- Austin, M. 2007. "Species Distribution Models and Ecological Theory: A Critical Assessment and some Possible New Approaches." *Ecological Modelling* 200: 1–19.
- Austin, M. P. 1985. "Continuum Concept, Ordination Methods, and Niche Theory." *Annual Review of Ecology and Systematics* 16: 39–61.

- Barnett, L. A. K., E. J. Ward, and S. C. Anderson. 2021. "Improving Estimates of Species Distribution Change by Incorporating Local Trends." *Ecography* 44: 427–39.
- Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. "The Crucial Role of the Accessible Area in Ecological Niche Modeling and Species Distribution Modeling." *Ecological Modelling* 222: 1810–9.
- Bellman, R. E. 1957. *Dynamic Programming*. Princeton, NJ: Princeton University Press.
- Beyer, H., D. T. Haydon, J. M. Morales, J. L. Frair, M. Hebblewhite, M. Mitchell, and J. Matthiopoulos. 2010. "The Interpretation of Habitat Preference Metrics under Use–Availability Designs." *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365: 2245–54.
- Beyer, H. L. H. L., E. Gurarie, L. Börger, M. Panzacchi, M. Basille, I. Herfindal, B. Van Moorter, S. R. Lele, and J. Matthiopoulos. 2016. "'You Shall Not Pass!': Quantifying Barrier Permeability and Proximity Avoidance by Animals." *Journal of Animal Ecology* 85: 43–53.
- Blonder, B. 2016. "Do Hypervolumes Have Holes?" *American Naturalist* 187: E93–E105.
- Blonder, B. 2018. "Hypervolume Concepts in Niche- and Trait-Based Ecology." *Ecography* 41: 1441–55.
- Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. "The n-Dimensional Hypervolume." *Global Ecology and Biogeography* 23: 595–609.
- Bolker, B. M. 2008. *Ecological models and data in R*. Princeton, NJ: Princeton University Press.
- Boyce, M. S., C. J. Johnson, E. H. Merrill, S. E. Nielsen, E. J. Solberg, and B. van Moorter. 2016. "Can Habitat Selection Predict Abundance?" *Journal of Animal Ecology* 85: 11–20.
- Boyce, M. S., and L. L. McDonald. 1999. "Relating Populations to Habitats Using Resource Selection Functions." *Trends in Ecology & Evolution* 14: 268–72.
- Boyce, M. S., L. L. McDonald, and B. F. J. Manly. 1999. "Relating Populations to Habitats-Reply." *Trends in Ecology & Evolution* 14: 490.
- Broennimann, O., M. C. Fitzpatrick, P. B. Pearman, B. Petitpierre, L. Pellissier, N. G. Yoccoz, W. Thuiller, et al. 2012. "Measuring Ecological Niche Overlap from Occurrence and Spatial Environmental Data." *Global Ecology and Biogeography* 21: 481–97.
- Carlson, B. S., S. Rotics, R. Nathan, M. Wikelski, and W. Jetz. 2021. "Individual Environmental Niches in Mobile Organisms." *Nature Communications* 12: 1–10.
- Carscadden, K. A., N. C. Emery, C. A. Arnillas, M. W. Cadotte, M. E. Afkhami, D. Gravel, S. W. Livingstone, and J. J. Wiens. 2020. "Niche Breadth: Causes and Consequences for Ecology, Evolution, and Conservation." *The Quarterly Review of Biology* 95: 179–214.
- Cassini, M. H. 2011. "Ecological Principles of Species Distribution Models: The Habitat Matching Rule." *Journal of Biogeography* 38: 2057–65.
- Chase, J. M. 2016. "Towards a Really Unified Theory for Metacommunities." *Functional Ecology* 19: 182–6.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. Dordrecht: Springer Science, Business Media BV, Formerly Kluwer Academic Publishers BV.
- Chesson, P. 1991. "A Need for Niches?" *Trends in Ecology & Evolution* 6: 26–9.
- Chesson, P., and C. T. Lee. 2005. "Families of Discrete Kernels for Modeling Dispersal." *Theoretical Population Biology* 67: 241–56.
- Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. "Resolving the Biodiversity Paradox." *Ecology Letters* 10: 647–59.
- Colwell, R. K., and E. R. Fuentes. 1975. "Experimental Studies of the Niche." *Annual Review of Ecology, Evolution, and Systematics* 6: 281–310.
- Colwell, R. K., and T. F. Rangel. 2009. "Hutchinson's Duality: The Once and Future Niche." *Proceedings of the National Academy of Sciences USA* 106: 19651–8.
- Courchamp, F., T. Clutton-Brock, and B. T. Grenfell. 1999. "Inverse Density Dependence and the Allee Effect." *Trends in Ecology and Evolution* 14: 405–10.
- D'Errico, F., W. E. Banks, D. L. Warren, G. Sgubin, K. Van Niekerk, C. Henshilwood, A. L. Daniau, and M. F. Sánchez Goñi. 2017. "Identifying Early Modern Human Ecological Niche Expansions and Associated Cultural Dynamics in the South African Middle Stone Age." *Proceedings of the National Academy of Sciences USA* 114: 7869–76.
- DeCesare, N. J., M. Hebblewhite, M. Bradley, D. Hervieux, L. Neufeld, and M. Musiani. 2014. "Linking Habitat Selection and Predation Risk to Spatial Variation in Survival." *Journal of Animal Ecology* 83: 343–52.
- Dennis, R. L. H. 2010. *A Resource-Based Habitat View for Conservation: Butterflies in the British Landscape*. Wiley-Blackwell. <https://www.wiley.com/en-ae/A+Resource+Based+Habitat+View+for+Conservation%3A+Butterflies+in+the+British+Landscape-p-9781444315264>.
- Diez, J. M., I. Giladi, R. Warren, and H. R. Pulliam. 2014. "Probabilistic and Spatially Variable Niches Inferred from Demography." *Journal of Ecology* 102: 544–54.
- Drake, J. M., C. Randin, A. Guisan, J. M. Drake, C. Randint, and A. Guisan. 2006. "Modelling Ecological Niches with Support Vector Machines." *Journal of Applied Ecology* 43: 424–32.
- Elith, J., and C. H. Graham. 2009. "Do They? How Do They? WHY Do They Differ? On Finding Reasons for Differing Performances of Species Distribution Models." *Ecography* 32: 66–77.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. "A Statistical Explanation of MaxEnt for Ecologists." *Diversity and Distributions* 17: 43–57.
- Farmer, J. D., E. Ott, and J. A. Yorke. 1983. "The Dimension of Chaotic Attractors." *Physica D: Nonlinear Phenomena* 7: 153–80.
- Fisher, R. 1930. *The Genetical Theory of Natural Selection*. New York: The Clarendon Press.
- Fretwell, S. D., and H. L. Lucas. 1969. "On Territorial Behavior and Other Factors Influencing Habitat Distribution in Birds – I. Theoretical Development." *Acta Biotheoretica* 19: 16–36.
- Gallien, L., T. Münkemüller, C. H. Albert, I. Boulangeat, and W. Thuiller. 2010. "Predicting Potential Distributions of Invasive Species: Where to Go from Here?" *Diversity and Distributions* 16: 331–42.

- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. "Application of Random Effects to the Study of Resource Selection by Animals." *Journal of Animal Ecology* 75: 887–98.
- Godsoe, W. 2010. "I can't Define the Niche but I Know it when I See it: A Formal Link between Statistical Theory and the Ecological Niche." *Oikos* 119: 53–60.
- Godsoe, W. 2012. "Are Comparisons of Species Distribution Models Biased? Are they Biologically Meaningful?" *Ecography* 35: 769–79.
- Godsoe, W., P. J. Bellingham, and E. Moltchanova. 2022. "Disentangling Niche Theory and Beta Diversity Change." *American Naturalist* 199(4): 510–22. <https://doi.org/10.1086/718592>.
- Godsoe, W., and L. J. Harmon. 2012. "How Do Species Interactions Affect Species Distribution Models?" *Ecography* 35: 811–20.
- Godsoe, W., J. Jankowski, R. D. Holt, and D. Gravel. 2017. "Integrating Biogeography with Contemporary Niche Theory." *Trends in Ecology and Evolution* 32: 488–99.
- Grinnell, J. 1917. "The Niche-Relationships of the California Thrasher." *The Auk* 34(4): 427–33.
- Guisan, A., and N. E. Zimmermann. 2000. "Predictive Habitat Distribution Models in Ecology." *Ecological Modelling* 135: 147–86.
- Hall, L. S., P. R. Krausman, M. L. Morrison, L. S. Hall, P. R. Krausman, and M. L. Morrison. 1997. "The Habitat Concept and a Plea for Standard Terminology." *Wildlife Society Bulletin* 25: 173–82.
- Hanski, I., and M. E. Gilpin. 1997. *Metapopulation Biology* 512. Cambridge, MA: Academic Press.
- Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. "Are Species' Range Limits Simply Niche Limits Writ Large? A Review of Transplant Experiments beyond the Range." *American Naturalist* 183: 157–73.
- Hastie, T., and R. Tibshirani. 1993. "Varying-Coefficient Models." *Journal of the Royal Statistical Society* 55: 757–96.
- Hirzel, A. H., and R. Arlettaz. 2003. "Modeling Habitat Suitability for Complex Species Distributions by Environmental-Distance Geometric Mean." *Environmental Management* 32: 614–23.
- Holbrook, J. D., L. E. Olson, N. J. DeCesare, M. Hebblewhite, J. R. Squires, and R. Steenweg. 2019. "Functional Responses in Habitat Selection: Clarifying Hypotheses and Interpretations." *Ecological Applications* 29: e01852.
- Holt, R. D. 1987. "On the Relation between Niche Overlap and Competition: The Effect of Incommensurable Niche Dimensions." *Nordic Society Oikos* 48: 110–4.
- Holt, R. D. 2009. "Bringing the Hutchinsonian Niche into the 21st Century: Ecological and Evolutionary Perspectives." *Proceedings of the National Academy of Sciences USA* 106: 19659–65.
- Holt, R. D., T. M. Knight, and M. Barfield. 2004. "Allee Effects, Immigration, and the Evolution of Species' Niches." *American Naturalist* 163: 253–62.
- Hubbell, S. P. 2004. "Reviewed Work(s): Ecological Niches: Linking Classical and Contemporary Approaches. Interspecific Interactions. By Jonathan M. Chase and Mathew A. Leibold." *Quarterly Review of Biology* 79: 96–7.
- Hurlbert, S. H. 1981. "A Gentle Depilation of the Niche: Dicean Resource Sets in Resource Hyperspace." *Evolutionary Theory* 5: 177–84.
- Hutchinson, G. E. 1978. *An Introduction to Population Ecology*. New Haven, CT: Yale University Press.
- Hutchinson, G. E. E. 1957. "Concluding Remarks." *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–27.
- Jackson, H. B., and L. Fahrig. 2015. "Are Ecologists Conducting Research at the Optimal Scale?" *Global Ecology and Biogeography* 24: 52–63.
- JasonMat. 2022. "JasonMat/FundamentalNiche: Ecological Monographs First View (v1.0)." Zenodo. <https://doi.org/10.5281/zenodo.6609762>.
- Jimenez, L., and J. Soberón. 2021. "Estimating the Fundamental Niche: Accounting for the Uneven Availability of Existing Climates." *Ecological Modelling* 464: 109823.
- Jiménez, L., J. Soberón, J. A. Christen, and D. Soto. 2019. "On the Problem of Modeling a Fundamental Niche from Occurrence Data." *Ecological Modelling* 397: 74–83.
- Jiménez-Valverde, A., J. M. Lobo, and J. Hortal. 2008. "Not As Good as they Seem: The Importance of Concepts in Species Distribution Modelling." *Diversity and Distributions* 14: 885–90.
- Johnson, D. H. 1980. "The Comparison of Usage and Availability Measurements for Evaluating Resource Preference." *Ecology* 61: 65–71.
- Jongejans, E., O. Skarpaas, and K. Shea. 2008. "Dispersal, Demography and Spatial Population Models for Conservation and Control Management." *Perspectives in Plant Ecology, Evolution and Systematics* 9: 153–70.
- Kearney, M., B. L. Phillips, C. R. Tracy, K. A. Christian, G. Betts, and W. P. Porter. 2008. "Modelling Species Distributions without Using Species Distributions: The Cane Toad in Australia under Current and Future Climates." *Ecography* 31: 423–34.
- Kearney, M., and W. Porter. 2009. "Mechanistic Niche Modelling: Combining Physiological and Spatial Data to Predict Species' Ranges." *Ecology Letters* 12: 334–50.
- Kearney, M. R., and W. P. Porter. 2004. "Mapping the Fundamental Niche: Physiology, Climate and the Distribution of a Nocturnal Lizard." *Ecology* 85: 3119–31.
- Kearney, M., S. J. Simpson, D. Raubenheimer, and B. Helmuth. 2010. "Modelling the Ecological Niche from Functional Traits." *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3469–83.
- Kindsvater, H. K., N. K. Dulvy, C. Horswill, M.-J. Juan-Jordá, M. Mangel, and J. Matthiopoulos. 2018. "Overcoming the Data Crisis in Biodiversity Conservation." *Trends in Ecology and Evolution* 33: 676–88.
- Kissling, W. D., C. F. Dormann, J. Groeneveld, T. Hickler, I. Kühn, G. J. McInerney, J. M. Montoya, et al. 2012. "Towards Novel Approaches to Modelling Biotic Interactions in Multispecies Assemblages at Large Spatial Extents." *Journal of Biogeography* 39: 2163–78.
- Lande, R. 1982. "A Quantitative Genetic Theory of Life History Evolution." *Ecology* 63: 607–15.
- Leibold, M. A. 2008. "Ecology: Return of the Niche." *Nature* 454: 39–41.
- Lele, S. R., and J. L. Keim. 2006. "Weighted Distributions and Estimation of Resource Selection Probability Functions." *Ecology* 87: 3021–8.
- Levin, S. A. 1992. "The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture." *Ecology* 73(6): 1943–67. <https://doi.org/10.2307/1941447>.
- MacNab, Y. C. 2018. "Some Recent Work on Multivariate Gaussian Markov Random Fields." *TEST* 27: 497–541.

- Malanson, G. P. 1997. "Simulated Responses to Hypothetical Fundamental Niches." *Journal of Vegetation Science* 8: 307–16.
- Manly, B. F. J., D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource Selection by Animals*. Dordrecht: Springer Netherlands.
- Martin, J., C. Calenge, P. Y. Quenette, and D. Allainé. 2008. "Importance of Movement Constraints in Habitat Selection Studies." *Ecological Modelling* 213: 257–62.
- Matthiopoulos, J. 2003. "The Use of Space by Animals as a Function of Accessibility and Preference." *Ecological Modelling* 159: 239–68.
- Matthiopoulos, J., J. Fieberg, and G. Aarts. 2020. "Species-Habitat Associations: Spatial Data, Predictive Models, and Ecological Insights." University of Minnesota Libraries Publishing: 103. Retrieved from the University of Minnesota Digital Conservancy. <https://hdl.handle.net/11299/217469>.
- Matthiopoulos, J., J. Fieberg, G. Aarts, F. Barraquand, and B. E. Kendall. 2020. "Within Reach? Habitat Availability as a Function of Individual Mobility and Spatial Structuring." *The American Naturalist* 195: 1009–26.
- Matthiopoulos, J., J. Fieberg, G. Aarts, H. L. Beyer, J. M. Morales, and D. T. Haydon. 2015. "Establishing the Link between Habitat Selection and Animal Population Dynamics." *Ecological Monographs* 85: 413–36.
- Matthiopoulos, J., C. Field, and R. MacLeod. 2019. "Predicting Population Change from Models Based on Habitat Availability and Utilization." *Proceedings of the Royal Society B: Biological Sciences* 286: 20182911.
- Matthiopoulos, J., M. Hebblewhite, G. Aarts, and J. Fieberg. 2011. "Generalized Functional Responses for Species Distributions." *Ecology* 92: 583–9.
- McGill, B. J. 2010. "Matters of Scale." *Science* 328: 575–6.
- McInerney, G. J., and R. S. Etienne. 2013. "'Niche' or 'Distribution' Modelling? A Response to Warren." *Trends in Ecology and Evolution* 28: 191–2.
- McInerney, G. J., and R. S. Etienne. 2012b. "Stitch the Niche—a Practical Philosophy and Visual Schematic for the Niche Concept." *Journal of Biogeography* 39: 2103–11.
- McInerney, G. J., and R. S. Etienne. 2012c. "Pitch the Niche—Taking Responsibility for the Concepts we Use in Ecology and Species Distribution Modelling." *Journal of Biogeography* 39: 2112–8.
- McInerney, G. J., and R. S. Etienne. 2012a. "Ditch the Niche—Is the Niche a Useful Concept in Ecology or Species Distribution Modelling?" *Journal of Biogeography* 39: 2096–102.
- McLoughlin, P. D., M. S. Boyce, T. Coulson, and T. Clutton-Brock. 2006. "Lifetime Reproductive Success and Density-Dependent, Multi-Variable Resource Selection." *Proceedings of the Royal Society B: Biological Sciences* 273: 1449–54.
- McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. "Considering Ecological Dynamics in Resource Selection Functions." *Journal of Animal Ecology* 79: 4–12.
- Merow, C., M. J. Smith, and J. A. Silander. 2013. "A Practical Guide to MaxEnt for Modeling species' Distributions: What it Does, and why Inputs and Settings Matter." *Ecography* 36: 1058–69.
- Moilanen, A., A. Wilson Kerrie, and H. P. Possingham. 2008. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford: Oxford University Press.
- Morales, J. M. M., P. R. R. Moorcroft, J. Matthiopoulos, J. L. L. Frair, J. G. G. Kie, R. A. A. Powell, E. H. H. Merrill, and D. T. T. Haydon. 2010. "Building the Bridge between Animal Movement and Population Dynamics." *Philosophical Transactions of the Royal Society B Biological Sciences* 365: 2289–301.
- Mouquet, N., Y. Lagadeuc, V. Devictor, L. Doyen, A. Duputié, D. Eveillard, D. Faure, et al. 2015. "Predictive Ecology in a Changing World." *Journal of Applied Ecology* 52: 1293–310.
- Muhly, T. B., C. A. Johnson, M. Hebblewhite, E. W. Neilson, D. Fortin, J. M. Fryxell, A. D. M. Latham, et al. 2019. "Functional Response of Wolves to Human Development across Boreal North America." *Ecology and Evolution* 9: 10801–15.
- Murray, B. G. 1985. "Population Growth Rate as a Measure of Individual Fitness." *Oikos* 44: 509.
- Mysterud, A., and R. A. Ims. 1998. "Functional Responses in Habitat Use: Availability Influences Relative Use in Trade-off Situations." *Ecology* 79: 1435–41.
- Nisbet, R. M., and W. S. C. Gurney. 2004. *Modelling Fluctuating Populations*. Caldwell, NJ: Blackburn.
- Nogués-Bravo, D. 2009. "Predicting the Past Distribution of Species Climatic Niches." *Global Ecology and Biogeography* 18: 521–31.
- Nur, N. 1984. "Fitness, Population Growth Rate and Natural Selection." *Oikos* 42: 413–4.
- Nur, N. 1987. "Population Growth Rate and the Measurement of Fitness: A Critical Reflection." *Oikos* 48: 338.
- Ollason, J. G. 1991. "What Is this Stuff Called Fitness?" *Biology and Philosophy* 6: 81–92.
- Osborne, P. E., G. M. Foody, and S. Suárez-Seoane. 2007. "Non-stationarity and Local Approaches to Modelling the Distributions of Wildlife." *Diversity and Distributions* 13: 313–23.
- Ovaskainen, O., and N. Abrego. 2020. *Joint Species Distribution Modelling: With Applications in R (Ecology, Biodiversity and Conservation)*. Cambridge, MA: Cambridge University Press.
- Pagel, J., and F. M. Schurr. 2011. "Forecasting Species Ranges by Statistical Estimation of Ecological Niches and Spatial Population Dynamics." *Global Ecology and Biogeography* 21: 293–304.
- Parentoni Martins, R. 2017. "To What Degree Are Philosophy and the Ecological Niche Concept Necessary in the Ecological Theory and Conservation?" *European Journal of Ecology* 3: 42–54.
- Paton, R. S., and J. Matthiopoulos. 2018. "Defining the Scale of Habitat Availability for Models of Habitat Selection." *Ecology* 97: 1113–22.
- Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. "Niche Dynamics in Space and Time." *Trends in Ecology and Evolution* 23: 149–58.
- Pedruski, M. T., G. F. Fussmann, and A. Gonzalez. 2016. "A Network Approach Reveals Surprises about the History of the Niche." *Ecosphere* 7: 1–12.
- Peterson, A. T., M. Papeş, and J. Soberón. 2015. "Mechanistic and Correlative Models of Ecological Niches." *European Journal of Ecology* 1: 28–38.
- Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martinez-Meyer, M. Nakamura, M. B. Araújo, et al. 2011. *Ecological Niches and Geographic Distributions*. Princeton, NJ: Princeton University Press.

- Pettersson, S., and M. Nilsson Jacobi. 2021. "Spatial Heterogeneity Enhance Robustness of Large Multi-Species Ecosystems." *PLoS Computational Biology* 17(10): e1008899. <https://doi.org/10.1371/journal.pcbi.1008899>.
- Phalan, B., M. Onial, A. Balmford, and R. E. Green. 2011. "Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared." *Science* 333: 1289–91.
- Pocheville, A. 2015. "The Ecological Niche: History and Recent Controversies." In *Handbook of Evolutionary Thinking in the Sciences*, edited by T. Heams, P. Huneman, G. Lecointre, and M. Silberstein, 547–86. Dordrecht: Springer.
- Pulliam, H. R. 2000. "On the Relationship between Niche and Distribution." *Ecology Letters* 3: 349–61.
- Roff, D. A. 2008. "Defining Fitness in Evolutionary Models." *Journal of Genetics* 87: 339–48.
- Rosenzweig, M. L. 1991. "Habitat Selection and Population Interactions: The Search for Mechanism." *The American Naturalist* 137: S5–S28.
- Rosenzweig, M. L., and Z. Abramsky. 1985. "Detecting Density-Dependent Habitat Selection." *American Naturalist* 126: 405–17.
- Rotenberry, J. T., K. L. Preston, and S. T. Knick. 2006. "GIS-Based Niche Modeling for Mapping Species' Habitat." *Ecology* 87: 1458–64.
- Roughgarden, J. 1974. "The Fundamental and Realized Niche of a Solitary Population." *The American Naturalist* 108: 232–5.
- Sales, L. P., M. W. Hayward, and R. Loyola. 2021. "What Do you Mean by 'Niche?'" Modern Ecological Theories Are Not Coherent on Rhetoric about the Niche Concept." *Acta Oecologica* 110: 103701.
- Sayer, J., T. Sunderland, J. Ghazoul, J. L. Pfund, D. Sheil, E. Meijaard, M. Venter, et al. 2013. "Ten Principles for a Landscape Approach to Reconciling Agriculture, Conservation, and Other Competing Land Uses." *Proceedings of the National Academy of Sciences USA* 110: 8349–56.
- Schurr, F. M., J. Pagel, J. S. Cabral, J. Groeneveld, O. Bykova, R. B. O'Hara, F. Hartig, et al. 2012. "How to Understand Species' Niches and Range Dynamics: A Demographic Research Agenda for Biogeography." *Journal of Biogeography* 39: 2146–62.
- Skellam, J. G. 1951. "Random Dispersal in Theoretical Populations." *Biometrika* 38: 196–218.
- Slack, N. G. 2011. *G. Evelyn Hutchinson and the Invention of Modern Ecology*. London: Yale University Press.
- Snyder, R. E., and P. Chesson. 2004. "How the Spatial Scales of Dispersal, Competition, and Environmental Heterogeneity Interact to Affect Coexistence." *American Naturalist* 164: 633–50.
- Soberón, J. 2007. "Grinnellian and Eltonian Niches and Geographic Distributions of Species." *Ecology Letters* 10: 1115–23.
- Soberón, J. 2014. "Commentary on Ditch, Stitch and Pitch: The Niche Is Here to Stay." *Journal of Biogeography* 41: 414–7.
- Soberón, J. M. 2010. "Niche and Area of Distribution Modeling: A Population Ecology Perspective." *Ecography* 33: 159–67.
- Soberón, J., and M. Nakamura. 2009. "Niches and Distributional Areas: Concepts, Methods, and Assumptions." *Proceedings of the National Academy of Sciences USA* 106: 19644–50.
- Soberón, J., and A. T. Peterson. 2005. "Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas." *Biodiversity Informatics* 2: 1–10.
- Soberón, J., and A. T. Peterson. 2020. "What Is the Shape of the Fundamental Grinnellian Niche?" *Theoretical Ecology* 13: 105–15.
- Stenseth, N. C. 1983. "Grasses, Grazers, Mutualism and Coevolution: A Comment about Handwaving in Ecology." *Oikos* 41: 152–3.
- Thuiller, W., M. B. Arau, and A. H. Hirzel. 2004. "Presence-Absence Versus Suitability-Only Modelling Methods for Predicting Bird Habitat Suitability." *Ecography* 4: 437–48.
- Tilman, D. 1980. "Resources: A Graphical-Mechanistic Approach to Competition and Predation." *The American Naturalist* 116: 362–93.
- Tilman, D., and P. Kareiva. 1997. *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*. Princeton, NJ: Princeton University Press.
- Tisdell, C., and I. Seidl. 2004. "Niches and Economic Competition: Implications for Economic Efficiency, Growth and Diversity." *Structural Change and Economic Dynamics* 15: 119–35.
- Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton, NJ: Princeton University Press.
- Warren, D. L. 2012. "In Defense of 'Niche Modeling'." *Trends in Ecology and Evolution* 27: 497–500.
- Warren, D. L. 2013. "'Niche Modeling': That Uncomfortable Sensation Means it's Working. A Reply to McNerny and Etienne." *Trends in Ecology and Evolution* 28: 193–4.
- Weimerskirch, H., M. Louzao, S. De Grissac, and K. Delord. 2012. "Changes in Wind Pattern Alter Albatross Distribution and Life-History Traits." *Science* 335: 211–4.
- Whittaker, R. H., S. A. Levin, and R. B. Root. 1973. "Niche, Habitat and Ecotope." *The American Naturalist* 107: 321–38.
- Yates, K. L., P. J. Bouchet, M. J. Caley, K. Mengersen, C. F. Randin, S. Parnell, A. H. Fielding, et al. 2018. "Outstanding Challenges in the Transferability of Ecological Models." *Trends in Ecology and Evolution* 33: 790–802.
- Yen, J. D. L., Z. Tonkin, J. Lyon, W. Koster, A. Kitchingman, K. Stamation, and P. A. Vesik. 2019. "Integrating Multiple Data Types to Connect Ecological Theory and Data among Levels." *Frontiers in Ecology and Evolution* 7: 1–7.
- Zurell, D., J. Elith, and B. Schröder. 2012. "Predicting to New Environments: Tools for Visualizing Model Behaviour and Impacts on Mapped Distributions." *Diversity and Distributions* 18: 628–34.

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