Reflections on an essential but elusive ecological metaphor: the Hutchinsonian niche

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Online supplement (with Michael Barfield**)** 4,649 words, five figures

Preamble. This essay was submitted to The American Naturalist on July 29, 2021. I received favorable reviews and editorial comments on October 12, 2024. was asked to shorten and restructure. For personal reasons, I have had to put this revision on the back-burner, but I do expect a shortened and modified version of this manuscript to appear in due course, with updated references. Colleagues have suggested I post the original package on the web, so that the ideas can be disseminated more broadly. I note that my long-time research Dr. Michael Barfield coauthored the technical supplement; he approves this document being placed in an online archive.

Abstract The Hutchinsonian niche, a pervasive metaphor in ecology, is a sister concept to Sewall Wright's adaptive landscape, with a shared focus on fitness. Characterizing what fitness means (and how to measure it) is a fundamental conceptual issue in both evolutionary biology and ecology. After a brief overview of adaptive landscapes and issues with fitness, this essay contrasts G.E. Hutchinson's 1978 formalization of the niche as a surface of intrinsic growth rate across environments, with his earlier 1957 formulation focused on population persistence across environments. The former has come to be a prevalent usage of "niche" discourse in the ecological and evolutionary literature, but the latter conceptualization warrants attention, if one for instance wishes to relate niche concepts to species' geographical distributions. Conceptualizing a species' niche as a surface of probabilities of persistence across environments requires consideration of factors beyond intrinsic growth rate when rare, including dispersal, demographic stochasticity, and density dependence, among other factors – all elements needed for the metaphor of the Hutchinsonian niche to fully capture its original meaning as a statement about what a species requires from its environment in order to persist.

“Perhaps our ultimate understanding of scientific topics is measured in terms of our ability to generate metaphorical pictures of what is going on. Maybe understanding *is* coming up with metaphorical pictures.” Bak (1996).

“If I can't picture it, I can't understand it.” — Albert Einstein, attributed to Einstein by physicist John Archibald Wheeler in Horgan (1991).

Introduction

Powerful metaphors, including visual images encapsulating key ideas, are central to scientific discourse (Bailer-Jones 2002). Metaphors can have problems (Silvertown 2016), including vagueness, reification, and the conceptual shackles of hidden assumptions. Nonetheless, metaphors provide inspiration and facilitate communication among scientists, as well as with the broader public (Olson et al. 2019), and play a crucial role in the construction of scientific theories. One of the most famous metaphors in evolutionary biology is the “adaptive landscape” of Sewall Wright (1932). Below, I touch on subtleties in terminology and usage, but in this essay I use the phrase “adaptive landscape” as an umbrella term, spanning several inter-related topographic metaphors in evolutionary biology (as do others, see e.g. Svensson and Calsbeek 2012). This visual metaphor evokes a vivid image of evolution as being akin to a hill walker (Wright 1959, p. 130) or mountain climber (Lewontin 1963) struggling ever upwards towards a peak. When a population has neared that peak, the adaptations of its members reflect the past action of natural selection culling out traits and genes of lower fitness (Rosales 2017). This essay is crafted as a belated response to receipt of the Sewall Wright Award from the American Society of Naturalists a few years back (received summer 2011), so I start with a short reflection on this enduring contribution of Wright to our discipline, before moving on to a related, equally pervasive ecological metaphor – the Hutchinsonian niche. As is the case for adaptive landscapes in evolutionary biology, the concept of “niche” is a metaphor (actually, more than one metaphor) that plays a central role in ecological thinking. The two metaphors are linked by a common concern with “fitness.”

I use simple models to make conceptual points, and along the way tie together different strands of the existing ecological literature, in I hope a novel and useful way. I will extend a cluster of ideas sketched briefly in Holt (2009a), outlining needed refinements in the Hutchinsonian niche concept, and in particular an expansion to encompass three missing ingredients: i. an explicit concern with space and movement; ii. stochasticity (both demographic and environmental); and iii. density dependence (direct, and indirect), encompassing the combination of that species' impacts on the environment, and feedbacks from those effects on the environment onto the species itself. The evolutionary dimension of the niche warrants attention, but this essay focuses on ecological issues. A companion essay (Holt, in prep.) grapples with intraspecific variation, conservatism and evolution in the niche, a topic squarely at the interface of ecology and evolutionary biology.

A meditation on Wright's adaptive landscape, and fitness: A preamble to the Hutchinsonian niche

Sewall Wright himself (A. Rosales, pers. comm.; e.g., p. 244, Wright 1942) invoked ecological niches as relevant to evolutionary outcomes, but as best I can discern, he does not explicitly define the term "niche," but rather uses it to denote (rather vaguely) ecological "opportunities," which could correspond to adaptive peaks in a surface of selective values. Wright himself seems not to have used the term "adaptive landscape," but other authors in the Modern Synthesis came close (and it is common for writers to refer to "Wright's adaptive landscape" as if he coined the term; e.g. Wade 2012). For instance, George Gaylord Simpson said "Wright … has suggested a figure of speech and a pictorial representation that graphically portray the relationship between selection, structure, and adaptation. The field of possible structural variation is pictured as a landscape with hills and valleys…" (p. 89, in the 1984 reprint edition), and Simpson utilized the notion of "adaptive zones" to interpret evolutionary patterns in the fossil record. Theodosius Dobzhansky (pp. 26-27, 1970) refers to "adaptive peaks," "adaptive valleys," and "topographic maps" in reference to Wright's ideas; in a seminal paper, Russ Lande (1976) tied together the perspectives of Simpson and Wright by focusing on "an adaptive topography for the average phenotype in a population." The first explicit usage of the term "adaptive landscape" that I can find is Lewontin and White (1960), who present "maps" of mean population fitness as a function of mean genotype frequency in an Australian grasshopper, and use the term “adaptive landscape” (with the phrase in quotes, without citations), suggesting this may indeed be the mutational event creating this minor cultural meme.

Natural selection may not always move populations towards higher average fitness (due to frequency dependence, multi-locus effects, etc.), but as Charlesworth and Charlesworth (2012, p. 63) remark, the adaptive landscape metaphor nonetheless “… provides a useful way of visualizing the action of selection in complicated situations.” The metaphor has enduring value well beyond Wright’s own focus on his shifting balance theory. As many authors have noted (e.g., Gavrilets 2004; Dietrich and Skipper 2012 and others in Svensson and Calsbeek 2012), the adaptive landscape metaphor arises in various renditions and terms (e.g., “surfaces of selective value,” Wright 1988; “fitness landscapes” Gavrilets 2004; as well as “adaptive landscapes,” e.g., Vincent and Brown 2005). Sometimes an adaptive landscape portrays the fitnesses of each of a set of individual genotypes or phenotypes (e.g. the “holey” fitness landscapes of Gavrilets 2004). Wright himself referred to “surfaces of selective value” (Wright 1988), which are fitnesses of individual genotypes, in an abstract space of genotypic possibilities. Populations have heritable variation in fitness, and so are represented as discs of varying sizes superimposed on this landscape (fig. 4 in Wright 1932). Sometimes, the landscape describes mean population fitness, as a function of gene frequency or mean phenotype in a population (Lande 1976; Fear and Price 1998; Arnold et al. 2001; Svensson and Calsbeek 2012; Hendry 2017). Indeed, Dan Bolnick (pers. comm.) suggests that current usage is largely for the term “fitness landscape” to refer to fitnesses of individuals (with a given phenotype and genotype), and “adaptive landscape” instead to denote population mean fitness as a function of mean phenotypes or gene frequencies. Despite such heterogeneity in meaning, and skepticism from some as to the utility or conceptual coherence of the term at all (e.g., Kaplan 2008; Pigliucci 2012), references to adaptive landscapes in one flavor or another pervade the current literature of evolutionary biology. Representative recent examples include Dickson and Pierce (2019), Voje (2020), and Anderson et al. (2021} (see Fragata et al. 2019 for a review). For instance, Brady et al. (2019a) added causal arrows to a figure of an adaptive landscape to creatively characterize different ways maladaptation might arise; Childs et al. (2004) constructed fitness landscapes for flowering time in a stochastic environment; Lawrence et al. (2019) drew on adaptive landscape imagery to interpret protective coloration in poison frogs; and, Kokko et al. (2017) reflect on how ecological and genetic complexities challenge simplistic views of adaptation as simply hill-climbing. All these authors find the adaptive landscape metaphor to have continuing value as a conceptual "hook" for their studies, providing a way to help shape theory development and to communicate complex and subtle ideas. As Skipper and Dietrich (2012) remark, the adaptive landscape is a robust heuristic in evolutionary theory.

Gavrilets (2004) perceptively notes that the fitness landscape describing the relationship of individual phenotype or genotype to fitness is more fundamental than that relating mean population fitness to mean phenotypic or genotypic state, for the former is required to derive the latter. Dan Bolnick has remarked to me, "Practically, we pretty much only ever empirically measure fitness landscapes, not adaptive landscapes." Evolutionary biologists typically focus on relative fitness, which drives changes in frequency of alternative alleles in selection (e.g., Orr 2009; Bertram and Masel 2019). Ecologists by contrast traffic in absolute fitness (Brady et al. 2019b). Even if selection is frequency-independent, because relative fitness of a given allele is measured as its absolute fitness in comparison to mean fitness in its population, relative fitness depends upon allele frequency (Orr 2007). The most straightforward rendition of fitness surfaces is absolute fitness or components of fitness of individuals (e.g., viability from birth to reproduction in a discrete generation model where individuals vary only in survival) as a function of their genotype or phenotype.

The metaphor of an adaptive landscape thus rests on a somewhat subtle (even slippery) concept – fitness (Wade 2012). English usage of the word "fit" broadly denotes either of two things: the aptness of an object or person for a particular role or task (e.g., the fit of a key to a lock), and the vigor or health of an individual (e.g., the fitness of a star athlete). There has been a long debate among biologists and philosophers about what the term "fitness" in an evolutionary context means and how it should be measured (e.g., Sober 2001; Ramsey and Pence 2013; Pence and Ramsey 2015), and the word has been used in biology in many ways, and quantified variously (Brommer 2000; Roff 2008). Dawkins (1982) in a chapter titled “An Agony in Five Fits” identified five distinct usages of “fitness” --and he would prefer to avoid the term “fitness” entirely.

Ultimately, the dynamics addressed by ecological and evolutionary theory rest on patterns of individual births and deaths across time and space (and changes in state in individuals between those events) for lineages of ancestors and their descendants, where those births and deaths (and state changes) are causally related to both the traits of organisms (and thus the genotypes that underly those traits), and their environments. A fitness metric provides a convenient shorthand of this complex nexus of causes, an emergent property, aggregate cause, or accounting summary of the flux of demographic events that drives both ecology and evolution, taking into accounts factors such as density and frequency dependence (Doebeli et al. 2017; Coulson et al. preprint). Characterizing what metric is appropriate, however, can be subtle. As Crewe et al. (2018) state, “The technical definitions of reproductive value and fitness, with all their apparatus, are complicated.” Indeed.

There have been long-standing debates about which combination of births and deaths provides the best fitness metric for understanding evolution; for instance, is it the intrinsic growth rate r, or lifetime reproductive success R (Pásztor et al. 1996; Metcalf and Pavard 2007; Roff 2008)? The two metrics can give different results about the expected outcome of selection. It is simplest to characterize fitness for clonal organisms, where in the absence of mutation genotypes move as a package across generations, but even here there are subtleties. The “phenotypic gambit” (Grafen 1984) in behavioral ecology and adaptive dynamics basically assumes that phenotypes are transmitted faithfully across generations (as is expected with asexual reproduction); with sex and recombination, however, the “environment” of a given allele or other heritable unit includes a shifting genetic environment, and so the realized fitness of any allele has to account for the effects of this genetic milieu, and the genotype-to-phenotype mapping. Rousset (2004, p. xvi) states that fitness is “the expected number of adult offspring of an adult” and Rice (2004, p. 6) comparably remarks “… fitness [is] the reproductive contribution of an individual to the next generation.” These are starting points, but not the end of the story (how does one define “adult,” for instance?). In populations with continuous, overlapping generations, Ronald Fisher (1930) considered fitness to be the Malthusian growth parameter (*r*), a population parameter, calculated from individuals' birth and death schedules (as well as reproductive values, which are population-level attributes, Charlesworth 1980, 1994; Grafen 2015). Current thinking (Metz et al. 1992; Metz 2014) has identified a general fitness metric called "invasion fitness." This is a generalization of exponential growth or decline, a dominant Lyapunov exponent, for example that of an ergodic multiplicative sequence of transition matrices describing population growth as time gets large, for a clone introduced at trace numbers into a persistent ancestral population (which implies the ancestor has an average long-term growth rate of zero). Sometimes this abstract quantity matches up with either the intrinsic growth rate, *r*, or lifetime reproductive success, *R*, depending upon assumptions made about density dependence and the magnitude of environmental fluctuations (Engen and Saether 2016). However, in many realistic scenarios (e.g., with temporally fluctuating environments, or with stage and/or spatial structure) these familiar proxies for fitness are inadequate for identifying those strategies that will be evolutionarily and convergently stable strategies (Orzack 1993; Metz 2014; Lion and Metz 2018).

Maynard Smith (1989, p. 38) remarks that ascribing fitness to individuals is not quite right "Fitness is a property, not of an individual, but of a class of individuals—for example of individuals homozygous for allele A at a particular locus. Thus the phrase 'expected number of offspring' means the average number, not the number produced by some one individual. If the first human infant with a gene for levitation were struck by lightning in its pram, this would not prove the new genotype to have low fitness, but only that the particular child was unlucky." The "class" that is most relevant, I suggest, is not any old class, but that comprised of lineages emerging from the successive ancestor-descendent relationships of individuals or heritable units (individual A begets individual B, who begets C, etc., or replicator A copies itself to A′, A″ etc.; Akcay and Van Cleve 2015, Queller 2020). The term "lineage selection" was first coined in the context of levels-of-selection issues (Nunney 1999), but a perspective on lineages (rather than solely individual organisms) pertains more broadly and indeed critically, I think, particularly when considering population dynamics and evolution in more complex environments. (One realistic complication that I mention, just to put aside, is that the trait may not be a fixed attribute such as a given body size, but a suite of trait values across environments – norms of reaction, expressions of phenotypic plasticity. These terms pertain to lineages experiencing a range of environmental settings, not a single individual in its own singular environment.) The structure of environmental variability influences the outcome of selection in heterogeneous environments, and in particular average reproductive success can fail as a fitness metric (Frank 2011). When there is variability in birth and death rates, over space, or through time, or as a function of social and genetic context, genealogical perspectives are required to make accurate evolutionary predictions (Graves and Weinreich 2017).

In any case, the basic idea underlying the adaptive landscape metaphor is that there is a mapping of evolutionary possibilities (lineages of alternative phenotypes or genotypes among which selection can draw) onto a fitness metric – for a given (and usually unspecified) environment. The shape of the adaptive landscape will often differ among fitness metrics, and considering how these shapes differ (e.g., in the position of optimal phenotypes) can help one perceive the different evolutionary implications of alternative metrics.

The evolutionary metaphor of the adaptive landscape, I suggest, is sister to a principal usage of the word ”niche” in ecology – with the twist that rather than expressing fitness as a function of genotype/phenotype, for a given environment, the Hutchinsonian niche is a fitness metric for a given genotype/phenotype (or lineage), as a function of environmental states (very broadly conceived). This function can often (but not always) be pictured visually as a landscape. It is not widely recognized (Mark McPeek, pers. comm.), but this Hutchinsonian niche concept (Holt 2009a) is at base the ecological counterpart to fitness surfaces or adaptive landscapes in evolutionary biology – maybe two sides of the same coin. Or, in a nod to the landscape metaphor, maybe they can be viewed as two complementary views of a unified fitness surface landscape (see fig. 3.13 in McPeek 2017). As we will see, issues about the choice of metrics of fitness, and the need to consider lineages rather than just individuals, pertain to niche concepts. One arena where the two metaphors diverge is that ecologists are concerned with persistence and extinction, which as we will see may involve considerations other than those that arise when considering the fitnesses that drive selection.

An ecological metaphor based on fitness – the Hutchinson niche

Many authors have provided excellent discussions of the history of the niche concept (or concepts) in ecology (e.g., Whittaker and Levin, 1975; Hurlbert 1981; Schoener 1989; Chase and Leibold 2003; Pedruski et al. 2016; Sales et al. 2021). My emphasis here is on its connection with demography. The original English meaning of the word "niche" denotes a concrete place, such as the cavity in a church wall where the statue of a saint resides. Elton (p. 64, 1927) made the word "place" more abstract and referred to niches as the "place in the community" of a species, like the role of a vicar in an English village. This sense lives on robustly in ecological discourse. As two examples among many that could be cited, Barraclough (p. 2, 2019) remarks that the causes of speciation include "… the availability of new ecological niches," and Gauzere et al. (2020) suggest that there are many vacant niches for tree species in central European forests. So, Elton's meaning of "niche" persists.

When a statue fills its niche, it preempts a space where another statue might instead reside. This is a form of "impact" of that first statue on its world. Understanding impacts of species on their environments (broadly defined) (Leibold 1995; Chase and Leibold 2003), and how those impacts in turn feed back onto the species themselves, is essential for understanding population regulation and species coexistence in interacting webs (Meszéna et al. 2006). Whittaker et al. (1973) suggested the word "niche" should refer just to the interactions of a species with other members of its local community, with "habitat" denoting its dependence on non-interactive environmental conditions (e.g., temperature), for instance influencing its geographical distributions. (These authors also suggested "ecotope" as a term encompassing both "niche + habitat"; the word is rarely used this way, and has acquired another distinct meaning in landscape ecology.) Hutchinson's own use of the word "niche" was in the context of community structure (competitive exclusion, species packing, etc.), but contemporary references to species' niches pervade discourse as well about the causes of species' geographical ranges over broad areas (e.g., Peterson et al. 2011), not just local community interactions.

Hutchinson (1957) re-cast usage of the term "niche" to provide a compact language for encapsulating what a species requires in the world in order to persist. He stated (p. 416) that the fundamental niche of a species is that suite of environmental states in which "every point … corresponds to a state of the environment that would permit the species … to exist indefinitely" (one presumes without recurrent immigration from external sources). His original rendition of this concept was set-theoretic (the famed "n-dimensional hypervolume", Blonder 2018; Blonder et al. 2018). Later, he linked his niche concept to the most basic concept of population ecology – exponential population growth or decline (Hutchinson 1978). Hutchinson (p. 194, 1978) envisaged that one could plot per capita birth and death rates $b(E)$ and $d(E)$ for a species with continuously overlapping generations as a function of a suite of environmental attributes (a vector, E, with elements such as e.g., mean daily temperature, pH, and predator abundance). Relevant environmental features in general include not just abiotic variables such as temperature, but also the abundance and trait values of interacting species, including the abundance and trait composition of the species itself. However, for many purposes, one focuses on a focal species when it is rare and density dependence is ignored. "Rarity" for example is assumed when analyzing invasibility in community ecology (McPeek 2017); the Hutchinsonian niche in its 1978 formulation is thus a visual map of invasibility. For the moment, we ignore realistic complications such as age and stage structure, spatial location, and the discreteness of individuals, and assume a constant environment over the time scales in question.

An abstract example is shown in figure 1. Demographic rates are functions of two environmental variables (these plots are "demographic response functions," *sensu* Pulliam 2000). Birth rates are a Gaussian bulging out of the page (fig. 1, left), whereas death rates are a parabola, sinking into the page (fig. 1, right) (light tones indicate "better," i.e., higher births, or lower deaths). The optimal environment for births differs from that for deaths. Stage-specific vital rates such as survival, fecundity, growth, and germination often do have distinct patterns of variation in response to environmental variation in space or time (Villellas et al. 2015; Pironen et al. 2018; Andrello et al. 2020), so discrepancies in which environments are optimal for different vital rates are likely quite general.

The difference between these two demographic rates, evaluated at low densities in a constant, closed environment, leads to the core model of population ecology, namely density-independent exponential growth,

$$\frac{dN}{dt} = r(E)N \text{, where}$$

$$r(E) = b(E) - d(E) \qquad (1)$$

where *r* is the intrinsic per capita rate of growth, and as before *E* is a vector of factors in the environment (very broadly conceived). As noted above with respect to "fitness" in evolutionary biology, these demographic rates are population attributes describing a lineage, not really properties of individuals. Expressed graphically against components of *E* (see fig. 2, left), equation (1) defines a *niche response surface* (e.g., fig. 12-4 in Hutchinson 1978, based on Maguire 1973) – which, metaphorically, is a landscape. (Some authors, such as Pásztor et al. 2016, avoid use of the word "niche" in this way, and instead refer simply to a species growth potential. I think current usage for now (but see Discussion) favors continued use of Hutchinson's term.) The exponential model for population growth provides the foundation upon which almost the entire elaborate edifice of theoretical ecology rests (Case 2000; Pásztor et al. 2016), if *E* is interpreted appropriately, with equations for the dynamics of each interacting species and for the abiotic components of ecosystems.

There is growing emphasis on this demographic perspective on species' niches in analyses of geographic ranges (Schurr et al. 2012). Almost always, the fitness metric used to characterize niche response surfaces is the instantaneous growth rate (eq. [1]) (e.g., Peterson et al. 2011, p. 27; representative citations include Merow et al. 2014; Greiser et al. 2020; Pagel et al. 2020; Treurnicht et al. 2020). The shape of the niche surface defined by equation (1) matters (see below), but in practice the focus has often been on the boundary subset of *E* where

$$r(E) = 0. \qquad (2)$$

This expression cleaves the world into two domains – those where a species should go extinct ($r(E) < 0$), and those where it might persist, deterministically ($r(E) > 0$). Expressed graphically, with *E* described by continuous Cartesian axes, in simple cases this is a bounded, compact set demarcating the set envisaged in Hutchinson (1957) (e.g., the oval describing the niche boundary in fig. 2, left). In more complex cases this simple geometric representation breaks down (e.g., in strongly seasonal environments, Soberón and Peterson 2020), reminiscent of the inadequacy of simple shapes for adaptive landscapes when considering complex genotype-to-fitness mappings (e.g., the ”holey” landscape of Gavrilets 2004).

The shape of the niche response surface, away from the niche boundary defined by (2), matters, not just that boundary. Sax et al. (2013), for instance, coin the term “tolerance niche” to denote environments in which populations are not self-sustaining, but individuals can survive for some period, and possibly reproduce to some degree. This might describe habitats with sink populations maintained by recurrent immigration (Holt 1985; Pulliam 2000; Keddy 1982; Loreau et al. 2013). The more gradual decline is in the sink, the more abundant is the population sustained there by immigration (Holt 1993). Within the niche boundary given by equation (2), niche shape and optima are important, for instance to tackle applied problems such as the effective control of invasive species. Near equilibrium, the shape of the niche response surface determines how sensitive population growth rate is to small environmental perturbations; such sensitivities enter into the environmental feedbacks that govern species coexistence (Meszéna et al. 2006), and determine how species respond to temporal environmental variation. Feedbacks also help determine equilibrial or average abundances, given persistence. Below I touch on this feedback aspect of the niche, but for now put it aside.

The emphasis on assessing demographic performance at low densities reflects the fact that Hutchinson viewed the niche as a summary of what a species needs to “indefinitely persist,” which means one focuses primarily on episodes when that species is pushed to low numbers, and then asks if it can increase and therefore persist. If a population is abundant, one assumes that over the short run, one need not worry about extinction – so the emphasis is on when it is rare. To a first approximation, characterizing the niche thusly describes conditions for invasibility of a community (ability to increase when rare), a central focus of community assembly and coexistence theory (McPeek 2017; HilleRis Lambers et al. 2012; the “invasion criterion” of Grainger et al. 2019). The protocol of describing the niche of a species as a surface of intrinsic growth rates across environments informs analyses of geographic range limits (e.g., Soberón 2010; Peterson et al. 2011; Eckhart, et al. 2011) and of the relationship of functional traits to community assembly (Laughlin et al. 2020; Treurnicht et al. 2020). A focus on demography is increasingly recognized as being essential for understanding the dynamics and limits of species' geographical ranges (Eckhart et al. 2011; Normand et al. 2014). Niche discourse focused on the environmental dependencies of the intrinsic growth rate provides a crisp way of talking about these issues.

Quantifying the Hutchinsonian niche in practice is challenging, because one has to measure growth rates across a range of environmental conditions. Though difficult (Holt 2009a; Laughlin et al. 2020), there are a growing number of examples quantifying demographic variables across geographical ranges both observationally (e.g. Treurnicht et al. 2016) and using experimental approaches such as transplants or lab measurements. Hooper et al. (2008) provide an excellent example of experimental quantification of key niche dimensions for *Daphnia magna* in Yorkshire, England. They brought a clone of this daphnid into the lab, initiated populations at low densities, and measured intrinsic growth rate as a function of two key abiotic variables of this zooplankter's niche – pH (important for osmotic balance of all aquatic organisms), and Ca^{2+} concentration (calcium is needed by crustaceans for their exoskeleton, shed frequently during development). They then compared the niche response surface of these lab populations to observed presences and absences across the permanent waterbodies of Yorkshire. Almost invariably, where the niche response surface predicted $r < 0$ for the observed chemistry of a waterbody, the zooplankter was absent. This illustrates how understanding a species' Hutchinsonian niche can be used to interpret distributional patterns.

Some authors have argued that the Hutchinsonian niche concept is so ambiguous and difficult to nail down that the term "niche" should be abandoned entirely (McInerny and Etienne 2012a; Angilletta et al. 2019). As with the adaptive landscape in evolutionary biology, one practical and conceptual challenge is that metrics of absolute fitness are aggregate properties of births and deaths within lineages. The actual causes of population change are individual births and deaths occurring in the different physical, biotic, and genetic environments of those individuals (Doebeli et al. 2017), as well changes in states (including spatial location) between these events, averaged in some apt fashion across the environments experienced by a lineage. This problem of accounting for heterogeneity in defining the niche for a lineage matches the conceptual problem noted above for adaptive landscapes (does the niche pertain to individuals, or instead to lineages?). The next section suggests one formal approach to constructing an appropriate average, accounting for the fact that different members of a lineage likely live in different places and so experience somewhat different environments. Another important issue, which I will not focus on here, is that within local populations and species there is likely heritable variation in niche properties, however the niche is defined. If that were not the case, then species would not evolve in their niches, and yet adaptive radiations show clearly that they do. In a companion essay (Holt in prep.), I will dwell on issues of intraspecific genetic variation in niches, and issues of niche conservatism and evolution, but here, I focus on conceptual issues that arise even for characterizing what counts as the "niche" of a single genetic clone.

Weaving dispersal into the Hutchinsonian niche

Expositions of the Hutchinsonian niche typically focus on the intrinsic per capita growth rate r, with no reference whatsoever to movement. For instance, in their fine monograph relating ecological niches to geographical distributions, Peterson et al. (2011, pp. 27-28) divide a geographical region occupied by a species into a spatially explicit grid of contiguous cells. Within each cell, one determines the local intrinsic growth rate; if positive, that cell is deemed to have an environment within that species' niche. Local dynamics can then be modified by movement among grid cells. This can be a useful approximation but is also in some ways misleading. Movement is essential to life at all scales (Nathan et al. 2008; Holt 2009b). Environments for most organisms are spatially heterogeneous. As Hutchinson (1959) remarked "… [one must consider] the mosaic nature of the environment. Except perhaps in open water when only uniform quasi- horizontal surfaces are considered, every area colonized by organisms has some local diversity [in habitat conditions] ." He remarks that how heterogeneity is experienced by an organism depends on its body size. It also (not explicitly noted by Hutchinson) depends upon how movement strategies filter the available environmental heterogeneity to define the actual, experienced environment of an organism even at small spatial scales. In general, biologists are better at measuring the traits of organisms than identifying and measuring the relevant feature of those organism's environments. As Levins (1979) noted, organisms "determine by their movements and physiological activity the effective statistical pattern of environment."

This observation pertains at all spatial scales. There is substantial variability in environmental conditions over short distances (e.g. 1 m^2 or less for plants in terrestrial systems), and variance in conditions grows with spatial scale (Lechowicz and Bell 1991; Bell et al. 1993; Richard et al. 2000). Microscale heterogeneity is experienced by almost all organisms, including rainforest denizens (Scheffers et al. 2017), soil taxa (Nunan et al. 2020), and bacteria in the open ocean (Stocker and Seymour 2012). Landscape heterogeneity can influence where species' range limits occur (Oldfather et al. 2019), and within species' ranges, there is substantial variability among sites in local densities, even at fine spatial resolutions, suggesting the impact of local heterogeneity in conditions (Holt et al. 2002). To characterize the Hutchinsonian niche across spatial scales, we need to focus on invasibility at each scale and take into account movements at each scale that govern how organisms bias their experience of their local environments. A formalism providing insights into scale dependence in the Hutchinson niche as modulated by movement is "scale transition theory" (e.g., Snyder and Chesson 2004; Chesson et al. 2005; Roy et al. 2005), described by Chesson (p. 52, 2012) as follows:

"Scale transition theory is an approach to understanding population and community dynamics in the presence of spatial or temporal variation in environmental factors or population densities. It focuses on changes in the equations for population dynamics as the scale enlarges. These changes are explained in terms of interactions between nonlinearities and variation on lower scales, and they predict the emergence of new properties on larger scales that are not predicted by lower scale dynamics in the absence of variation on lower scales."

How can scale transition theory inform the ecological niche concept, across spatial scales? Godsoe et al. (2017) suggest the following protocol. Consider a large, spatially closed continuous area, subdivided into a grid of n contiguous cells, among which individuals disperse (this procedure could also be carried out within each cell, leading to a hierarchy of nested cells; we will not explore this elaboration here). There is spatial heterogeneity, so birth and/or death rates vary among cells. Local population growth within grid cell k ($k = 1, \dots , n$), with environment E_k is (net local growth) + (inflow, I_k) – (outflow, O_k), or

$$\frac{dN_k}{dt} = r_k(E_k)N_k + I_k - O_k. \tag{3}$$

What are the regional dynamics of the entire population? If we assume dispersal among cells comes without cost (i.e., no death during movement; Kortessis and Holt (ms.) refine this formalism to encompass such costs), we can simply add up (3) over all localities; inputs and outputs cancel out. Using standard definitions of means and covariances leads to

$$\frac{d\overline{N}}{dt} = \overline{rN} = (\overline{r} + \mathrm{cov}(r,v))\overline{N} = \overline{r}_s\overline{N}. \tag{4}$$

Here $\overline{r}$ is the spatial average intrinsic growth of the species (the average is over cells), v is the fraction of the total population found in each locality, and $\mathrm{cov}(r,v)$ is the covariance between local r and that fraction. The quantity

$$r_s(E,v) = \overline{r} + \mathrm{cov}(r(E),v) \tag{5}$$

is the instantaneous growth rate of the population at the landscape scale, where E is a vector of local environmental conditions (which can vary among cells across the grid).

The spatial average growth rate suffices to characterize the Hutchinsonian niche if the covariance term is near zero. This occurs given i) negligible spatial heterogeneity in growth rates, ii) rapid, uniform movement across the landscape, homogenizing the spatial distribution of individuals, or iii) spatial variation in abundance arising for reasons uncorrelated with spatial variance in local growth rates. But often, none of these hold. Even if the spatially averaged growth rate across the landscape is negative, the population as a whole may nonetheless grow if the covariance term is positive and sufficiently large. So, at a broad scale, the landscape is within that species' Hutchinsonian niche. This can happen with passive dispersal (see below), and is enhanced with active, adaptive habitat selection, where individuals preferentially seek out sites with higher expected fitness (Schmidt 2004; Schmidt and Massol 2019). Conversely, the covariance term may be sufficiently negative that, even with a positive spatial average growth rate, the species fails to persist. In a constant environment, if all growth rates are negative, the the overall growth rate will still be negative; the covariance term matters given spatial heterogeneity, if growth is positive in some local sites and negative at others, as might be expected near range margins (Godsoe et al. 2017). In temporally varying environments, however, the overall growth rate can be positive, even if the average local growth rate is negative (Roy et al. 2005; and see below).

Expression (5) does not completely characterize a niche response service, because v is not yet determined. In some cases, there is a "preferred" value for v. In equation (3), let the birth and death rate at each location be constant, i.e., no density dependence or temporal variation, and also assume per capita movement rates are density-independent; "output" and "input" are then linear functions of local densities. The dynamics now match a system of linear ordinary differential equations,

$$\frac{d\overrightarrow{N}}{dt} = A\overrightarrow{N} \tag{6}$$

where $\overrightarrow{N}$ is a vector of local densities, and A is a square matrix. The diagonal elements of A are per capita (local growth – emigration) rates, and the off-diagonal elements are immigration rates (A_{jk} is the per capita movement rate out of j into k). In a temporally constant environment, the population eventually settles into a stable stage (= among-location) distribution (Caswell 2006), growing at a rate determined by the dominant eigenvalue of A. The stable habitat distribution is the right eigenvector of A. If this eigenvector is substituted for v in expression (5), we have a compact (if schematic) expression for the long-term growth rate of the species across a landscape. In graphical depictions of the niche, niche axes should in some fashion capture spatial variation in local growth rates, and the emergent imprint of covariation of local abundances with local growth rates. Because of the covariance term, rates and pattern of dispersal are implicitly embedded in the absolute fitness of a lineage across the environments it encounters, and so can influence the shape of the overall niche response surface.

After a species invades, there will often be a transient phase during which its realized growth rate changes, because the population has not yet reached its stable stage (spatial) distribution. After this transient phase, with random, non-directional dispersal, more individuals will occur in local sites with higher growth rates. This implies positive covariance between local abundance and local growth, so the regional growth rate may be positive, even though the spatially averaged local growth rate is negative, and even if the initial rate of decline happened to be negative (because the species was not yet in its stable stage distribution). In a temporally constant environment, this requires that some sites have a positive local growth rate (below, we touch on temporally variable environments, in which a species may persist in a landscape even if its long-term growth rate in each site is negative.) Figure 3 shows a simple example for two habitats with different intrinsic growth rates. At high movement rates, the population asymptotically experiences the spatial average growth rate (which is negative). At lower movement, relatively more individuals occupy the better habitat, and growth is positive. If individuals directionally disperse towards or stay in microenvironments with higher growth rates (Schmidt 2004; Schmidt and Massol 2019; Resetarits et al. 2019, Matthiapolous 2021), this further facilitates persistence in spatially variable environments. Thus, local patterns of movement are woven into the emergent birth and death rates that determine persistence.

Asymmetric dispersal can generate negative covariances between local growth rates and local density. Keddy (1982) described a clear example of such a negative covariance for the sea rocket *Cakile edentula* in Nova Scotia sand dunes. The sea rocket is denser mid-dune than seaward. One might surmise that growth rates are higher mid-dune, but Keddy showed the instantaneous growth rate is actually negative there across all densities. By contrast, growth rates were positive near the sea. This puzzling spatial pattern arises because a persistent wind from the ocean strips seeds near the beach, lowering density there, and deposits them inland in the dune, boosting abundance there. This generates a negative spatial covariance between local growth rate and local density. An increase in average wind speed might cause extinction, because of an aggravated mismatch of local abundance and growth rates.

Therefore, given spatial heterogeneity in environmental conditions, understanding the "indefinite persistence" of a species at any given spatial scale (Hutchinson 1957) requires paying close attention to patterns and rates of movement at finer scales of spatial resolution, not just spatial average birth and death rates. The scale transition expression (5) does not fully capture all the ways movement influences niches. In the future, the formalism should account for the demographic costs of movement (Kortessis and Holt ms.). Moreover, many lifestyles mandate shuttling among habitats, because of seasonal variation (e.g., migratory species, Holt and Fryxell 2011) or complex life histories where different stages use different habitats (e.g., McCoy et al. 2009), or because of local extinctions mandating recurrent colonization for persistence in a metapopulation context (Hanski 1999); this dependence of persistence on movement strategies was dubbed "stitching the niche" in Holt (2009a). [McInerny and Etienner 2012b use the phrase "stitch the niche" differently, to exhort the reader to ponder how they use the term "niche," and then "fix it up."] Matthiapolous (2021) has recently also argued that movement in heterogeneous environments can alter the shape of the fundamental niche, and used this to inform interpretation of the spatial distribution of the house sparrow. The bottom line is that the patterns and fitness consequences of dispersal at lower spatial scales implicitly enter into determining the shape and boundary of the niche response surface at a higher spatial scale. Movement ecology (Nathan et al. 2008) should be woven more fully into the ecological niche concept than it is at present. Whether or not this suggestion, when fully developed, permits simple visual renditions of niche surfaces (the landscape niche metaphor) remains to be determined.

The ecological niche as a surface of persistence probability across environments

Now, I return to the most basic equation in ecology (exponential growth, eq. [1]) and point out a subtlety in how one relates demography to species' niches, pertinent to our meditation on Hutchinson's (1957) view of the niche as those environments "permitting persistence." I have briefly touched on the debate in evolutionary biology about alternative fitness metrics. Likewise, one can use the vital rates of births and death in different ways than usual to characterize niches. Above (as is typical in ecology and biogeography, e.g. Hooper et al. 2008; Soberon 2010), the intrinsic growth rate $r = b - d$ was the measure of absolute fitness used to define a niche response surface (e.g., fig. 2a). Yet, this same simple population model (1) has another measure of absolute fitness, which can imply niche response surfaces differing substantially in shape, and which may better characterize persistence across environments.

Given the assumptions of model (1) for exponential growth or decline, an individual is expected to live $1/d$ time units, during which it reproduces at rate b. So the total expected number of offspring per individual over its lifetime (which in behavioral ecology is called lifetime reproductive success, and in epidemiology, the basic reproductive ratio), is

$$R(E) = \frac{b(E)}{d(E)}. \tag{7}$$

A simple graphical way to envisage the relationship between r and R away from equilibrium is shown in figure 4, where two complementary families of our two fitness metrics (r and R) describing exponential population growth or decline are plotted in a parameter space of birth and death rates (assumed constant). The family of lines comprised of parallel lines with slope 1 correspond to different values of the intrinsic growth rate $r = b - d$. The family of lines radiating from the origin correspond to values of the alternative fitness metric, $R = b/d$, with slopes $1/d$. The only members of these two families of lines coinciding are $r = 0$, and $R = 1$ (when a population is in equilibrium, deterministically). For any $r \neq 0$ or $R \neq 1$ (i.e., away from equilibrium), for any value of one metric there are an infinite number of alternative values of the other metric. Below, we argue that for a given r, extinction risk is higher in the direction shown by the arrow, where high values of b go along with high values of d, because for a given r, these vital rate combinations imply a lower R.

For now, we focus on the different niche response surfaces implied by this alternative fitness metric. One can construct a niche response surface using R instead of r. This has no effect on the deterministic conditions for persistence versus extinction, because $r > 0 \Leftrightarrow R > 1$, and $r < 0 \Leftrightarrow R < 1$. So the set of environments allowing "indefinite persistence" might be expected to be the same. But the overall shape of the niche response surface for populations away from equilibrium can differ sharply between the two fitness metrics, because the two metrics depend upon births and deaths in different ways. Figure 2 juxtaposes these alternative niche response surfaces, for the abstract demographic profiles of figure 1. The optimal environment for r differs from that for R. Moreover, the niche response surfaces are asymmetric, with the sharpest change in r for shifts in environmental conditions to the left – opposite to the asymmetry in R.

Does this matter? I suggest this difference in niche shapes given by the two complementary fitness metrics for exponential growth has real consequences for a causal understanding of species' distributions. Recall that Hutchinson's (1957) verbal statement of what a niche "is" emphasizes *persistence*. Much of community ecology rests on invasion analyses – the ability of species to increase, when rare, as measured by deterministic instantaneous rates of increase, as in equation (1) (e.g., MacArthur 1972; McPeek 2017; Grainger et al. 2019). There is a huge literature crafted around this protocol, yet there is increasing attention being given to ascertaining the role of demographic and environmental stochasticity in determining the outcome of interspecific interactions (e.g. Pedruski et al. 2015). There is a lively ongoing debate in coexistence theory as to whether or not the rate of invasion adequately measures persistence in competitive interactions (Jeltsch et al. 2019; Pande et al. 2020; Ellner et al. 2020; Schreiber et al. 2020). The basic issue, however, does not require one to grapple with the complexity of community interactions; it arises, quite simply, for a single species all on its own, in the absence of interspecific interactions. In the next few paragraphs, I suggest that rather than intrinsic growth rate r, one might envisage niche responses surfaces as probabilities of persistence across environments (over some time scale, and conditional on initial conditions), and an alternative fitness measure such as R might be more informative about persistence than is r.

My suggestion means that niche theory should be fused with population extinction theory. There is a huge literature on the mathematics of population extinction (key references include MacArthur and Wilson 1967; Leigh 1981; Foley 1994; Ludwig 1996; Orzack 1997; Lande et al. 2003, Lande and Orzack 1988; Ovaskainen and Meerson 2010; Carlson et.al. 2019), but there is, as yet, scant connection between that literature and niche concepts. This is an important direction for future development. If we reconceptualize niches as statements about probabilities of persistence, we need to specify our assumptions about initial conditions, to define the time scale over which persistence is gauged, and to recognize that no single measure of "fitness" may suffice to characterize persistence across environments. Density-dependent processes regulating abundance for instance are important, not only metrics of growth rate when rare. Here, I just touch on a few conceptual issues and use a simple model to illustrate these points about initial conditions, time scale, and fitness metrics, and then turn to density dependence.

Interpreted literally, Hutchinson's encapsulation of the niche as those environments where a species "exists indefinitely" would mean that species do not have niches at all! The reason is simply that all individuals die, there is a non-zero probability that any individual will not have offspring before its death, and populations are bounded (which must hold, given conservation of mass in our finite world). Given these very general propositions, extinction is inevitable as one lets time go to infinity (Jagers 1992; Halley and Iwasa 1998; Haccou et al. 2005). This might be a well-nigh astronomical span of time, but it will happen. As John Maynard Keynes famously quipped, "In the long run, we are all dead." Thus, in using the term "indefinitely" one must implicitly refer to some time scale over which persistence us to be gauged, starting with some assumed initial condition.

Classic results from branching processes and more recent extinction theory help sharpen this suggestion. Consider the seminal results of Kendall (1948), who presented a model that may be the earliest extinction model in ecology. Kendall examined a population growing with density-independent demographic rates in continuous time (for textbook presentations, see Allen 2011, pp. 251-253, and Renshaw 2013, pp. 74-76). We start at time $t = 0$ with a single individual in a clonal species. Given $n(t)$ individuals at time t, Kendall assumed the probability in dt of a birth is $b(t)n(t)dt$, and of a death is $d(t)n(t)dt$. We assume the environment is constant, so $b(t) = b$, and $d(t)=d$, and ignore density dependence. Kendall showed the probability that the initial individual has at least one descendent at some later time T (i.e., its lineage persists up to then) is

$$P_{survival} = \frac{R-1}{R-e^{-rT}} . \tag{8}$$

As T gets large, then if $b < d$, asymptotically $P_{survival} = 0$, whereas if $b > d$,

$$P_{survival} = 1 - \frac{1}{R} . \tag{9}$$

Thus, outside the niche as defined in terms of $r < 0$, extinction is inevitable. But, within the niche as usually defined ($r > 0$), persistence is not guaranteed, but depends on the fitness metric R.

Figure 5A shows the probability of long-term persistence for an asexual colonist, within its Hutchinsonian niche defined as $r > 0$, as a function of r and d. For a suite of species with the same positive r, those with high births and deaths leading to a lower R are more likely to suffer extinction. At low r, persistence is quite sensitive to d. In figure 4, those species in an equivalency class as measured by r fall along a line of slope 1; to the right along the arrow (along a line of constant r) in figure 4, R declines, and so does the probability of persistence. Thus, a suite of species with identical values for r can differ strongly in their probability of persistence. The intrinsic growth rate still matters in a transient phase, as it influences how quickly the asymptotic probability of persistence is reached (see eq. [8]).

Rather than using only intrinsic growth rate r, I suggest we might conceptualize complementary niche response surfaces as probabilities of persistence across environments. In crafting such surfaces, one might consider using alternative metrics having to do with persistence, such as expected mean or median times to extinction. Grimm and Wissel (2004) usefully observe that in many models of extinction dynamics, after an initial transient phase there is a negative exponential distribution of times to extinction. The characteristic time scale of exponential decay describing times to extinction might constitute an "intrinsic time to extinction," and this could be used to construct niche response surfaces. The online Supplement examines mean and median times to extinction for the above model. For the remainder of this essay, for simplicity, I focus on the probability of persistence, as a function of environmental variables (for given initial conditions and time scales), as a niche response surface.

Environmental dependencies in vital rates will determine the shape and peak of these niche response surfaces, but they may have different shapes than surfaces based on intrinsic growth rates. There is growing empirical evidence that environments with the highest probability of occurrence need not be those with the highest population growth rates (e.g., Thuiller et al. 2014). Figure 5B uses the schematic example of figures 1 and 2 to depict such a surface, based on expression (9). In this abstract example, the environment where persistence is most likely differs from that with the highest expected intrinsic growth rate. There are challenges in empirically implementing this suggestion for refining the Hutchinsonian niche (in effect returning to Hutchinson 1957), as it requires more knowledge about population dynamics and history than one usually has. The above model nonetheless usefully illustrates two simple points about characterizing niche response surfaces as probabilities of persistence: the need to be explicit about time scale, and the importance of specifying initial conditions. After touching on these, I then turn the third key ecological ingredient needed for re-interpretation of the Hutchinsonian niche based on probability of persistence: density dependence, in various flavors.

Time scale.

The simple expression (9) is an extrapolation to large T. Over shorter time scales, both r and R enter into the probability of persistence after colonization (expression [8]). Ideally, one would keep track not of a single metric of fitness, but its component (and causally underpinning) birth and death rates, since both have distinct influences on persistence. So, we see that even in this classic model, i. intrinsic growth rate (r) need not map neatly onto the probability of persistence, ii. alternative fitness metrics (R) may be more informative about persistence, iii. sometimes multiple metrics are required, and iv. a specification of time scale is needed to quantify the probability of persistence. Time scale is even more important when there is temporal environmental variability, since one must gauge persistence not just in a fixed environment, but along trajectories of shifting environmental states.

Initial conditions.

We have considered a specific initial condition: a lineage spawned by a single, clonally reproducing colonist introduced into a stable environment, ignoring density dependence. If instead there are n colonists, and they and their descendants do not experience density dependence among themselves, then each lineage spawned by a single colonist grows independently. So, the probability of establishment, per colonizing episode, is

$$P_e = 1-(1-P_{survival})^n \qquad (10)$$

If there are I independent introduction events, each with n colonizing propagules, we can replace n in equation (10) with In. With a large number of colonists aggregated over time, given a non-zero probability of persistence for a solitary colonist, expression (10) will approach unity; a species should thus be expected to quickly fill all its niche, i.e., all sites with $r > 0$ should be occupied, if dispersal is unlimited.

However, in dispersal-limited species, having one to just a few dispersers in rare colonization bouts might be typical; such species might thus be expected to be absent from many sites within their niche, based on their intrinsic growth rate. This is particularly likely where R is low. For a given r, extinction rather than persistence is more likely after a single colonization bout with few colonizers, for species with a “fast” lifestyle (high b and d), than for species with a “slow” lifestyle (low b and d) (i.e., comparing species along the arrow in fig. 4). When there is population structure (e.g., age or stage dependence in vital rates), one also needs to specify the initial structure of the invasive propagule to determine the probability of persistence. The online Supplement provides two worked examples demonstrating the importance of initial conditions and persistence, one for a population with stage structure (juveniles and adults), the other for a population introduced into two distinct habitats, coupled by dispersal.

The conceptual framework of ecology does not usually emphasize historical contingencies and context. Spencer (2020) has recently emphasized the importance of considering history in ecology, including the temporal arc of construction (e.g., routes of community assembly, priority effects, Fukami 2015), long transients and nonequilibrial dynamics, and the potential for alternative states. It is a historical contingency if colonization at a location typically involves rare bouts of very low numbers of dispersing individuals, rather than frequent episodes with many. This is the usual assumption in analyses of community assembly, and frequently arises in invasion biology. But ecologists and biogeographers are often concerned with populations that seem to be already well-established. This is another reasonable initial condition that one can assume (itself reflecting historical contingency) for characterizing a species' niche, and considering it brings me to the next topic.

Density dependence

Populations persisting over many generations will necessarily be bounded in their abundance, and fluctuate around a long-term mean abundance, their "carrying capacity." This requires feedbacks of population size on either birth or death rates (Royama 1992), mediated through abiotic and biotic factors (e.g., depletion of essential resources supply, aggravation of natural enemy attacks, buildup of toxins). Such feedbacks strongly influence persistence. The web of direct and indirect density dependencies within and between species are at the core of coexistence theory (Pásztor et al. 2016), but issues of feedbacks and equilibrial abundance are not normally captured in the "requirement" dimension of standard niche theory, but rather (in part) in the "impact" facet of the niche (Leibold 1995; Chase and Leibold 2003). All else being equal, if two (non-interacting) species have the same intrinsic growth rate when rare, the one with weaker density dependence should increase to higher abundance, and thereby be more likely to persist over longer time scales.

The flip side of persistence is, of course, extinction. A huge literature in mathematical ecology explores the role of population size and density dependence on extinction, starting with MacArthur and Wilson (1967) and many authors since. This is a large, complex, and not fully resolved topic, and I will not pretend to summarize it comprehensively. As Barbour (p. 189 in Haccou et al. 2005) states, "… Unfortunately, the expected time to extinction is a quantity that depends very much on the detail of the random processes that govern the population size. Simple rules of thumb are unreliable, except perhaps as qualitative guides…" Here I will just touch on a few such qualitative rules-of-thumb from this rich body of literature, suggesting what else needs to enter into the formulation of niche surfaces, construed as surfaces of probabilities of persistence across environments.

Allee effects

Given strong Allee effects (positive density dependence in growth rates at low densities; Keitt et al. 2001; Courchamp et al. 2008), even in a deterministic world there can be strong effects of initial conditions on establishment and persistence. Some Allee effects are immediate (e.g., the need for sexual partners to find each other, or for a prey species to be sufficiently abundant to satiate a predator). Others may be time-lagged, via shifts in the external environment that benefit a species increasingly over time, because of its own impacts on the environment (including at times long feedback loops). Drake (2014) for instance describes a power-law distribution of times to extinction in experimental water flea populations, and he ascribes this pattern to directional amelioration of the environment due to changes in the microbiota, induced by the water fleas themselves. This pattern differs sharply from the negative exponential distribution of times to extinction observed in nearly all formal extinction models. Most extinction theory to date does not address how a species might cause directional changes in its environment (possibly with long time lags) that in turn alters its own extinction risk. Drake's results suggests an emergent, time-lagged Allee effect. In Holt (2009a), I suggested one implication of strong, positive density dependence (direct or indirect) is that the range of environments in which a species can persist, once established and at reasonable abundance for a while (what I called the "persistence niche"), may exceed those where it can establish successfully in the first place when initially rare (the "establishment niche"). Peay (2016) notes that interspecific mutualisms are quite likely to generate this pattern; if species A benefits from the presence of species B, and A facilitates B, species A thereby indirectly positively affects itself, with time lags mediated through population responses. Allee effects magnify the importance of historical contingencies (hysteresis, Petraitis 2013) and landscape configuration (Keitt et al. 2001) in determining how species' niches map onto geographical ranges. Stable range limits can arise in patchy environments, even in the absence of environmental gradients (Keitt et al. 2001). (One empirical challenge arises in gauging the importance of Allee effects from population time series is that demographic stochasticity at low densities can lead to patterns resembling those expected from Allee effects (Lande 1998; Lande et al. 2003).)

Constraints on abundance

Ultimately, species stop growing because of negative density dependence, either depressing births, or boosting deaths (or both). Given density-independent growth up to some population size K, above which the population stops growing, with demographic stochasticity alone (as in the Kendall 1948 model above), classic results suggest the mean time to extinction T_e scales with K as

$$T_e = ce^{aK} \qquad (11)$$

(Lande 1993; Ovaskainen and Meerson 2010). The original analyses leading to equation (11) used Fokker-Planck approaches, which can be problematic in capturing the effects of large fluctuations (which often precipitate extinction). More recent analyses employing the Wentzel-Kramers-Brillouin approximation (from physics, e.g., Doering et al. 2005) account for such fluctuations, and lead to insights that differ in detail, but qualitatively still match this classic result. Expressions for mean time to extinction (e.g., eq. [1] in Ovaskainen and Meerson 2010) often involve the reproductive ratio R, as well as the equilibrial population size K of the related deterministic model. Expressions such as (11) imply that populations with a small carrying capacity do have a short time to extinction, but even modestly abundant populations, once established, can persist for a very long time scale, particularly if they have large R.

The "once established" comment here warrants further consideration, in terms of the niche metaphor. If the initial condition is one or a few individuals in rare colonizing episode in any given location, extinction may be likely and occupancy low, even in environments where, once near carrying capacity, persistence is expected to stretch to a very long time scale. This brings out the importance of being explicit about the initial conditions assumed in characterizing the Hutchinsonian niche. The niche space relevant to a high probability of initial invasion may well be much more constrained than that describing the persistence of already well-established populations. In an applied context, the "niche" relevant to invasion biology might differ from that needed in the management and conservation of populations already at hand.

Equation (11) pertains to a constant environment, but not to temporally variable environments, where it greatly overestimates the expected time to extinction. The influence of population size on persistence is sharply amplified given temporal variation in vital rates and carrying capacity, in which case: "extinction risk scales roughly as the inverse of the expected population size in taxa affected by moderate environmental stochasticity" (Hanski and Ovaskainen 2000; see also Ovaskainen and Meerson 2010). The word "roughly" here indicates this is a rule-of-thumb, not a precise quantification of extinction risk (Otso Ovaskainen, pers. comm.). Fluctuations in birth or death rates can push an initially large population to low levels, where it can then random walk by demographic stochasticity to extinction. Positive temporal autocorrelation in the environment in particular aggravates extinction risks, because a species can experience long spells at low densities (Haccou and Vatutin 2003).

There are several messages one can draw from this body of extinction theory. One is that in environments near the edge of niche space (low r and/or R), occupancy should be ragged, particularly given temporal variation pushing populations occasionally to low numbers. It is notable that many absences in the *Daphnia* study of Hooper et al. (2008) do involve sites with low (albeit positive) intrinsic growth rates. Another is that sculpting a niche surface in terms of probability of persistence is inherently multivariate: one needs to pay attention not only to fitness metrics such as local growth rates and reproductive ratios, but also to average abundances, and to measures of temporal variation in such fitness metrics and abundance (variance, autocorrelation, and particularly extrema), not just means.

This multivariate determination of the probability of persistence might be simplified, given tight correlations among these population attributes. The nature of such correlations (and even their sign), however, is the subject of vigorous debate. Martinez-Meyer et al. (2013) and Osorio-Olvera et al. (2020) for instance report that sites near the center of a species' ecological niche (where its intrinsic growth rate is presumably highest) also have higher abundances than do more peripheral sites (see also Brown 1984). In such cases, sites near the edge of niche space should be particularly prone to local extinctions, because the combination of low r and low K implies sharply aggravated extinction risk. Other authors by contrast find that local growth rates and abundances are often poorly or even negatively correlated (McGill 2012;

Santini et al. 2019). Thuiller et al. (2014) for instance report that high occurrence probability is associated with high local carrying capacity, but that if anything it was negatively correlated with intrinsic growth rate. Pironen et al (2017) reviewed empirical assessments of the "centre-periphery" hypothesis and concluded that although occupancy often seemed reduced in ecologically marginal habitats (compared to the center of a species' niche), there were no consistent patterns in abundance within occupied sites, or in demographic rates. There are a number of reasons why intrinsic growth rate might not correlate strongly with average or equilibrial abundance (Osorio-Olvera et al. 2019; Holt 2020). The reason this matters in the current context is that in such cases, intrinsic growth rate may be a misleading metric of extinction risk, and hence by itself be a poor predictor of occupancy (which reflects the probability of persistence).

Given that a population persists over a reasonable time scale, its births should roughly match its deaths. There is no reason to expect these demographic rates in quasi-equilibrial populations always to line up squarely with births and deaths at low densities at those same locations (i.e., the ability to grow when rare). (Indeed, if they do, it is a puzzle why the population persists at all, since its intrinsic growth rate will be near zero.) This is a challenge for empirical analyses across species' ranges: without paying careful attention to density dependence, it may be difficult to interpret observed patterns in abundance and occupancy across space. Holt (2020) used a simple model to highlight what might underlay discrepancies reported in the literature between intrinsic growth rate and local abundances. Assume a species locally follows a logistic growth equation at each location *i*:

$$\frac{dN_i}{dt} = N_i(r_i(E_i) - f_i(E_i)N_i) \tag{12}$$

Here, $r_i(E_i)$ is intrinsic growth rate, and $f_i(E_i)$ the strength of density dependence, both of which may depend on local environmental conditions. At equilibrium, $N_i^* = r_i(E_i) / f_i(E_i)$. Now, assume density dependence is spatially uniform, so $f_i(E_i) = f'$. Then, local equilibrial abundance should faithfully track local intrinsic growth rates. Sites with low values for r_i (and likely, R_i) will have low densities.

Populations at such sites should be vulnerable to extinction if N_i* is low, because of demographic stochasticity, aggravated by low growth rates. Therefore, with constraints on dispersal, occupancy should be low, given spatially uniform density dependence.

However, in general it is unlikely that the strength and functional form of density dependence will be spatially invariant (Holt 2020). Direct and indirect channels of density dependence reflect many contingent and spatially variable causal factors, such as renewal rates of depletable resources, and population and behavioral responses of natural enemies, each with their own independent responses to the environment, differing from that of $r_i(E)$. Macroecological studies of species distributions suggest that across the range of widespread species, at the majority of locations where a species occurs, its numbers can be quite low (Brown et al. 1995). If such differences among locations persist over time, spatial variation in abundance likely in part reflects spatial variation in the strength of density dependence. If f_i varies independently of r_i, one would not observe a strong relationship between equilibrial abundance and niche position, measured in terms of growth rate when rare. In other words, intrinsic growth rate might be a poor predictor of the probability of long-term persistence.

Fast growth rates can even endanger local persistence – given time-lagged density dependence

Occupancy (reflecting persistence over reasonable time scales) and growth rate when rare might not only be decoupled, but inversely related. When a population grows rapidly, it can overshoot its carrying capacity, and crash, endangering its persistence. Reindeer were introduced into St. Matthew Island off Alaska, grew exponentially at a rapid rate – and then plummeted to extinction, once they overexploited their slowly renewing plant food supply (Klein 1968). In a continental setting, if this happens in a number of locations coupled by dispersal (but not enough to be synchronized), this strong consumer-resource interaction can persist nonetheless as a metapopulation (viz., “stitching the niche” *sensu* Holt 2009a, as in Huffaker 1958’s classic experiments with mites on oranges). Ovaskainen et al. (2016) developed a butterfly metapopulation model (motivated by the famed Glanville fritillary system of the Aland Islands) where in each locale, butterfly dynamics fit the Ricker model. In this model, density dependence is over-compensatory and time-lagged (e.g., due to over-exploitation of depletable biotic resources), and an increase in the intrinsic growth rate leads to population cycles or even chaos, with excursions to low densities. Their model shows that across the landscape, patches that are higher quality (i.e., higher intrinsic growth rate), if occupied, do show greater average abundance. However, these patches in aggregate also have lower occupancy, because population overshoots followed by crashes generate heightened, sporadic extinction risks (see fig. 3.11, p. 92 in Ovaskainen et al. 2016). In epidemiology, pathogens with high *R* introduced into naïve host populations can overexploit the supply of susceptible hosts and go extinct more rapidly than do pathogens facing host populations with partial immunity; the latter pathogens have a lower initial growth rate when rare, but also are not as prone to burn rapidly through the supply of susceptible hosts, leading to extinction (Pulliam et al. 2007). Resource-consumer systems where the resource is alive, and the consumer highly effective at consumption, quite generally are prone to such "niche destruction" (Holt 2009a), leading to a potential inverse relationship between occupancy and intrinsic growth rates over part of niche space.

Putting the pieces together: crafting a more robust theory of the ecological niche.

Here, I have revisited ideas that I sketched in Holt (2009a), articulating how the enduring niche metaphor of Hutchinson (1957) – a characterization of those environments that permit persistence of a species – could be enriched, in the light of our current understanding of population processes. Here I briefly recapitulate the main points dwelt on above.

One issue is a reconsideration of dispersal. Many authors recognize that mismatches between species' distributions and niche requirements (Pulliam 2000; Pagel et al. 2020) can reflect dispersal. On the one hand, dispersal barriers can prevent good habitat from ever being occupied, and on the other, dispersal can sustain sink populations despite local growth rates being persistently negative. Above, I argued that beyond these sensible observations, a consideration of movement across scales is required to characterize a species' niche in the first place, since patterns of movement influence how local variability in the environment even at fine scales is translated into the aggregate, spatially averaged demographic rates that enter into fitness metrics.

The instantaneous intrinsic growth rate *r* when rare, though necessary, is not sufficient for understanding the niche as a landscape of probability of persistence across environments. Even for exponential growth in a constant environment, the branching process model of Kendall (1948) reveals an alternative fitness metric (lifetime reproductive success, or finite reproductive ratio, *R*) to be more informative about persistence. In epidemiology, *R* characterizes performance of an infectious disease agent across environments. Mordecai et al. (2019) for example examine how *R* varies as a function of temperature for vector-borne infectious diseases and use this thermal dependency to make predictions about how disease prevalence will shift with climate change. Such results provide first-order predictions about when epidemics – or more broadly introductions during community assembly – will likely fade out, versus persist, along gradients in temperature.

Moreover, given that all populations are bounded, understanding density-dependent feedbacks and long-term average abundance is essential to flesh out the niche concept of Hutchinson (1957) in terms of persistence. This requires integrating niche theory with the rich theory of extinction in population ecology. The niche metaphor interpreted as a statement about persistence may help provide a conceptual framework for this integration. Schreiber et al. (2020) recently evaluated conditions for joint persistence (viz., coexistence) in a guild of serpentine annual plants and concluded that "ecologists must look beyond invasion growth rates and consider species equilibrium population sizes." This empirical finding matches my conceptual suggestion. Understanding feedbacks is particularly relevant to persistence given positive density dependence at low numbers (Allee effects), or time-lagged negative density dependence, which can ensure that populations with high initial growth rates seal their own fate. Alirio Rosales (pers. comm.) has suggested that one could possibly revisit the adaptive landscape, and cast it in terms of persistence, rather than the more usual fitness metrics. Another way of stating this, I think, is that fitness metrics, ideally, should include the imprint of demographic stochasticity.

There are various ways one could put together the elements of space, stochasticity, and density dependence so as to refine the theory of the niche, keeping in mind the metaphor of the niche as an expression of performance (e.g. persistence) as a function across a space of environmental factors.

Hutchinson (1959) referred to the “mosaic” nature of the environment. Because there is always temporal variability, spatial (i.e., “real”) landscapes are not merely mosaics, but “kaleidoscopes” of constantly shifting local conditions. Because temporal variability can lead to local extinction, even if the long-term local growth rate in a closed population is positive (Lewontin and Cohen 1969), dispersal is often key to long-term persistence (the central insight underlying metapopulation ecology). We have assumed temporally constant growth rates, but scale transition approaches and expressions comparable to equation (4) also describe population dynamics in spatiotemporally varying environments (Roy et al. 2005). At a local level, in a closed population positive autocorrelation in the environment increases extinction risk, because populations are forced through runs of bad years (Haccou and Vatutin 2003). But if dispersal couples a number of such populations that are unsynchronized, local positive autocorrelation can facilitate metapopulation persistence. Given some dispersal, but not so much as to homogenize abundances across space, and particularly with temporally autocorrelated variation not completely synchronized across space, species will be temporarily more abundant where there are runs of good years and provide immigrants to other locales with later runs of good years. This can facilitate persistence, even if every location is on average a sink habitat (Jansen and Yoshimura 1998; Roy et al. 2005; Matthew and Gonzalez 2007). Expressions such as equation (5) still describe regional growth (Roy et al. 2005), but the covariance term now reflects temporal variation in local growth rates.

Kortessis et al. (2020) apply this insight to the spread of pandemics in human populations – an epidemic can spread if the local reproductive ratio of the infectious disease varies asynchronously among locations, coupled by movement, even though on average, disease control in each location would predict eradication. So, a region as a whole may be within the Hutchinsonian niche, even though each locale within it has properties that on average are outside the niche, seemingly dooming the species to extinction. A comprehensive extinction theory, combining all the ingredients of space and dispersal, demographic stochasticity, environmental variation in space and time, and feedbacks determining density-dependent constraints on abundance, is as yet *terra incognita* in theory-land (however, see Ovaskainen et al. 2020 for recent derivations of extinction thresholds for systems with localized dispersal and demographic stochasticity). Characterizing the niche requirements of a species in terms of its long-term persistence will also require that attention be paid to factors such as the availability and configuration of patches in landscapes, and the degree to which they are synchronized, as well as feedbacks in the context of interacting species. With demographic stochasticity, initial conditions (i.e., the site and stage of an introduced propagule) are important in determining persistence probability (see online Supplement). I do not pretend that in this essay I have provided the definitive theory that combines all these disparate elements into a cohesive whole. Rather, I have tried to put before you, the reader, the ingredients I think are needed for such a satisfactory theory – a desideratum for future work. I believe that the niche metaphor will continue to play a valuable heuristic role in tying these disparate elements into a cohesive theoretical whole.

One general methodological message is that in linking demography to distributions, it is valuable to keep track of births and deaths, separately, as much as possible, rather than just combining them immediately into net growth rates or reproductive ratios, because these distinct vital rates likely have different causal relationships with environmental conditions, and different consequences for persistence, versus extinction. Another general issue is that it may not be enough to focus on what a species immediately needs to grow when rare – for persistence over multi-generational scales, one has to consider effects of inertia and delayed feedbacks from the environment, leading to overshoots, resource depletion, unstable natural enemy-victim interactions, and the like, as well. The niche, conceived as a statement about probabilities of persistence of populations, has tendrils into and back from the world, mandating a holistic perspective, well beyond just what individuals in a species need immediately to survive and reproduce.

Following Hutchinson (1978), I (Holt 2009a) and others (e.g. Peterson et al. 2011) use the term “Hutchinsonian niche” to denote a niche response surface, where the response variable is the intrinsic growth rate of a species across environments. This rendition of the niche is close to that of Wright’s adaptive landscape, since both rest on a shared metric of fitness. This is the usage that may be most pertinent to the themes of niche conservatism and evolution (Wiens et al. 2010), since birth, death, and movement rates as functions of the environment are abstract traits with heritable variation among lineages, fueling evolution. Maybe we need another term for another kind of "landscape" – portraying a surface of the probability of persistence of a lineage across environments (conditioned on initial conditions and time scale), which is closer to Hutchinson's 1957 verbal description of the niche. In Holt (2009a) I used the term "persistence niche," but in a different and narrower way. Maybe that could suggestion could be modified. How about "probabilistic niche"? Not particularly euphonious, alas. I leave this as an open challenge for some young wordsmith.

I started this essay with quotes and a brief meditation on the powerful pull of visual metaphors such as the adaptive landscape of Sewall Wright, and the ecological niche of G.E. Hutchinson. Both are abstractions with compelling visual expressions – powerful heuristics that help guide thinking about the complex dynamical processes at play in ecology and evolution, and that facilitate conceptual integration – related by their mutual dependence upon a fitness metric. In some cases (e.g., clonal growth), that metric may be the same, but in others it might well differ, because population geneticists and evolutionary biologists more broadly are concerned with comparative, relative fitness within persisting populations, whereas ecologists focus on absolute fitness and in particular persistence, versus extinction, of populations. Variation in the environment that affects absolute fitness of individuals, but not the relative fitness of alternative genotypes and phenotypes within populations, clearly enters into the probability of persistence, but not the action of natural selection. The fusion of the two landscapes suggested above (see also McPeek 2017) may in the end be a kind of mirage that dissolves on closer inspection, because of the distinct aims of our two disciplines.

The utility of visual graphs that describe the niche as a surface of probabilities of persistence should be tried on for size, to determine its utility. I have argued that multiple population metrics (intrinsic growth rate, R, average abundance) and context (initial conditions, time scale) all enter into determining the probability of persistence. The environment can influence each of these, and different components could matter more in some circumstances, or questions (e.g., invasion biology vs. conservation), than in others. How organisms relate to environments (including other species), and how that relationship determines the dynamics that govern organic diversity, the spatial distribution of taxa, and the abundance of populations, is a central, unifying issue of ecology and evolutionary biology. The visual metaphor of the Hutchinson niche, I believe (as with Wright's adaptive landscape), provides a perennially helpful conceptual tool for helping clarify how we think through the implications of this tangled web of causal relationships and aim towards conceptual synthesis.

Acknowledgements

I thank Dan Bolnick for prompting me, kindly but firmly, to finish this essay, after a long gestational time lag, and commenting on an early draft. I thank Mike Barfield for helping with figure preparation and analyses contained in the Appendix – and for more than two decades of intellectually astute support assistance, and collaboration, for which I am deeply grateful. I thank Mark McPeek, Alirio Rosales, and Jorge Soberon for discussions on topics pertinent to this essay, and thoughtful edits. I thank Vitrell Sherif for help with references and manuscript preparation. I think the University of Florida Foundation for its support.

References:

Akcay, E. and J. Van Cleve. 2015. There is no fitness but fitness, and the lineage is its bearer. Philosophical Transactions of the Royal Society B 371:20150058.

Allen, L. J.S. 2011. An Introduction to Stochastic Processes with Applications to Biology, 2nd ed. CRC Press, Boca Rotan, Florida.

Anderson, D.W., F. Baier, G. Yang and N. Tokurii. 2021. The adaptive landscape of a metallo-enzyme is shaped by environment-dependent epistasis. Nature Communications 12:3867 | https://doi.org/10.1038/s41467-021-23943-x | www.nature.com/naturecommunications

Andrello, M., P. de Villemereuil, M. Carboni, D. Busson, M.-J. Fortin, O.E. Gaggiotti, and I. Till-Bottraud. 2020. Accounting for stochasticity in demographic compensation along the elevational range of an alpine plant. Ecology Letters 23:870-880.

Angilletta, J.J., Jr., M.W. Sears, O. Levy, J.P. Youngblood and J.M. VandenBrooks. 2019. Fundamental flaws with the fundamental niche. Integrative and Comparative Biology 59:1038-1048.

Arnold, S.I., M.E. Pfrender and A.G. Jones. 2001. The Adaptive Landscape as a conceptual bridge between micro- and macroevolution. Genetica 112:9-32.

Bailer-Jones, D.M. 2002. Models, metaphors and analogies. Pages 108-122 *in* P. Machamer and M. Silberstein, eds. The Blackwell Guide to the Philosophy of Science. Blackwell Publishers, Oxford, UK.

Bak, P. 1996. How Nature Works: The Science of Self-organized Criticality. Copernicus. Gottingen, Germany.

Barraclough, T.G. 2019. The Evolutionary Biology of Species. Oxford University Press. Oxford, UK.

Bell, G., M.J. Lechowicz, A. Appenzeller, M. Chandler, E. DeBlois, L. Jackson, et al. 1993. The spatial structure of the physical environment. Oceologia 96:114-121.

Bertram, J. and J. Masel.2019. Density-dependent selection and the limits of relative fitness. Theoretical Population Biology 128:81-92.

Blonder, B. 2018. Hypervolume concepts in niche- and trait-based ecology. Ecography 41:1441-1455.

Blonder, B., C.B. Morrow, B. Maitner, D.J. Harris, C. Lamanna, C. Violle, et al. 2018. New approaches for delineating *n*-dimensional hypervolumes. Methods in Ecology and Evolution 9:305-319.

Brady, S.P., D.I. Bolnick, A.L. Angert, , R.D.H. Barrett., A. Gonzalez, E. Crispo, et al. 2019a. Causes of maladaptation. Evolutionary Applications 12:1229-1242.

Brady, S.P., D.I. Bolnick, R.D.H. Barrett, L. Chapman, E. Crispo, A.M. Derry, et al. 2019b. Understanding maladaptation by uniting ecological and evolutionary perspectives. American Naturalist 194:495-515.

Brommer, J.E. 2000. The evolution of fitness in life history theory. Biological Reviews 75:377-404.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124:255-279.

Brown, J.H., D.W. Mehlman and G.C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028-2043.

Carlson, C.J., K.R. Burgio, T.A. Dallas and Wayne M. Getz. 2019. The mathematics of extinction across scales: from populations to the biosphere. Pages 225-264 *in* H. Kaper and F. Roberts, eds. Mathematics of Planet Earth. Springer International Publishing, Switzerland.

Case, T.J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press, Oxford, UK.

Caswell, H. 2006. Matrix Population Models: Construction, Analysis, and Interpretation. Oxford University Press. Oxford, UK.

Charlesworth, B. 1980, 2nd edition, 1994. Evolution in Age-structured Populations. Cambridge University Press, Cambridge, UK.

Charlesworth, B. and D. Charlesworth. 2012. Elements of Evolutionary Genetics. Roberts and Company, Publishers, Greenwood Village, Colorado.

Chase, J.M. and M.A. Leibold. 2003. Ecological Niches: Linking Classical and Contemporary Approaches. The University of Chicago Press: Chicago, Illinois.

Chesson, P. 2012. Scale transition theory: Its aims, motivations and predication. Ecological Complexity 10:52-68.

Chesson, P., M.J. Donahue, B.A. Melbourne, A.L.W. Sears. 2005. Scale transition theory for understanding mechanisms in metacommunities. Pages 279-306 *in* M. Holyoak, M.A. Leibold, R.D. Holt, eds. Metacommunities: Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago, Illinois.

Childs, D.Z., M. Rees, K.E. Rose, P.J. Grubb and S.P. Ellner. 2004. Evolution of size-dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model. Proceedings of the Royal Society B 271:425-434.

Coulson, T., T. Potter, A. Felmy. 2020. Fitness functions, genetic and non-genetic inheritance, and why ecological dynamics and evolution are inevitably linked. bioRxiv https://doi.org/10.1101/762658

Courchamp, F., L. Berec, and J. Gascoigne. 2008. Allee Effects in Ecology and Conservation. Oxford University Press, Oxford, UK.

Crewe, P., R. Gratwick, and A. Grafen. 2018. Defining fitness in an uncertain world. Journal of Mathematical Biology 76:1059-1099.

Dawkins, R. 1982. The Extended Phenotype: The Gene as the Unit of Selection. W.H. Freeman and Company, Oxford University Press, Oxford, UK.

Dickson, B.V. and S.E. Pierce. 2019. Functional performance of turtle humerus shape across an ecological adaptive landscape. Evolution 73:1265-1277.

Dietrich, M.R. and R.A. Skipper, Jr. 2012. A shifting terrain: a brief history of the adaptive landscape. Pages 3-15 *in* E.I. Svensson and R. Calsbeek, eds. The Adaptive Landscape in Evolutionary Biology. Oxford University Press. Oxford, UK.

Dobzhansky, T. Genetics and the Evolutionary Process. 4th ed. 1970. Columbia University Press, New York, NY.

Doebeli, M., Y. Ispolatov and B. Simon. 2017. Towards a mechanistic foundation of evolutionary theory. eLife 6:e23804. doi: 10.7554/eLife.23804.

Doering, C.R., K.V. Sargsyan, and L.M. Sander. 2005. Extinction times for birth-death processes: Exact results, continuum asymptotics, and the failure of the Fokker-Planck approximation. Multiscale Model. Simulation. 3:283-299.

Drake, J.M. 2014. Tail probabilities of extinction time in a large number of experimental populations. Ecology 95:1119-1126.

Eckhart, V.M., M.A. Geber, W.F. Morris, E.S. Fabio, P. Tiffin and D.A. Moeller. 2011. The geography of demography: long-term demographic studies and species distribution models reveals a species border limited by adaptation. American Naturalist 178: S26-S34.

Ellner, S.P., R.E. Snyder, P.B. Adler, G. Hooker and S.J. Schreiber. 2020. Technical comment on Pande et al. (2020): Why invasion analysis is important for understanding coexistence. Ecology Letters 23:1721-1724.

Elton, C.S. 1927. Animal Ecology. Sidgwick and Jackson, London, UK.

Engen, S. and B.-E. Saether. 2016. r- and K-selection in fluctuating populations is determined by the evolutionary trade-off between two fitness measures: Growth rate and lifetime reproductive success. Evolution 71:167-173.

Fear, K.K. and T. Price. 1998. The adaptive surface in ecology. Oikos 82:440-448.

Fisher, R.A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, UK.

Foley, P.1994. Predicting extinction times from environmental stochasticity and carrying capacity. Conservation Biology 8:124-137.

Frank, S.A. 2011. Natural selection. I. Variable environments and uncertain returns on investment. Journal of Evolutionary Biology 24:2299-2309.

Fragata, I., A. Blanckaert, M.A.D. Louro, D.A. Liberles and C. Bank. 2019. Evolution in the light of fitness landscape theory. Trends in Ecology and Evolution 34:69-82.

Fukami, T. 2015. Historical contingency in community assembly: Integrating niches, species pools, and priority effects. Annual Review of Ecology, Evolution, and Systematics. 46: 1-24.

Gavrilets, S. 2004. Fitness Landscapes and the Origin of Species. Princeton University Press. Princeton, New Jersey.

Godsoe, W., J. Jankowski, R.D. Holt and D. Gravel. 2017. Integrating biogeography with contemporary niche theory. Trends in Ecology and Evolution 32:488-499.

Grafen A (1984) Natural selection, kin selection and group selection. In: Krebs J, Davies N (eds) Behav Ecol. Blackwell, Oxford, pp 62–84

Grafen, A. 2015. Biological fitness and the fundamental theorem of natural selection. American Naturalist 186:1-14.

Grainger, T.N., J.M. Levine and B. Gilbert. 2019. The invasion criterion: A common currency for ecological research. Trends in Ecology and Evolution 34:925- 935.

Gauzere, P., X. Morin, C. Violle, I. Caspeta, C. Ray and B. Blonder. 2020. Vacant yet invasible niches in forest community assembly. Functional Ecology 34:1945-1955.

Graves, C.J. and D.M. Weinreich. 2017. Variability in fitness effects can preclude selection of the fittest. Annual Review of Ecology, Evolution, and Systematics 48:399-417.

Greiser, C., K. Hylander, E. Meineri, M. Luoto, and J. Ehrlén. 2020. Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. Ecography 43:637-657.

Grimm, V. and C. Wissel 2004. The intrinsic mean time to extinction: a unifying approach to analyzing persistence and viability of populations. Oikos 105:501-511.

Haccou, P. and V.A. Vatutin. 2003. Establishment success and extinction risk in autocorrelated environments. Theoretical Population Biology 64:303-314.

Haccou, P., P. Jagers and V.A. Vatutin. 2005. Branching Processes: Variation, Growth, and Extinction of Populations. Cambridge University Press, Cambridge, UK.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford UK.

Hanski, I. and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape Nature 404:755-758.

Halley, J. and Y. Iwasa. 1998. Extinction of a population under both demographic and environmental stochasticity. Theoretical Population Biology 53:1-15.

Hendry, A.P. 2017. Eco-Evolutionary Dynamics. Princeton University Press. Princeton, New Jersey.

HilleRisLambers, J., P.B. Adler, W.S. Harpole, J.M. Levine and M.M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics 63:227-248.

Holt, R.D. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28: 181-208.

Holt, R.D. 1993. Ecology at the mesoscale: The influence of regional processes on local communities. Pages 77-88 *in* R. Ricklefs and D. Schluter, eds. Species Diversity in Ecological Communities. University of Chicago Press, Chicago, Illinois.

Holt, R.D. 2009a. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. Proceedings of the National Academy of Sciences, USA 106: 19659–19665.

Holt, R.D. 2009b. Darwin, Malthus, and movement: A hidden assumption in the demographic foundations of evolution. Israel Journal of Ecology and Evolution 55: 189-198.

Holt, R.D. 2020. Reflections on niches and numbers. Ecography 43:387-390.

Holt, R.D. and J.M. Fryxell. 2011. Theoretical reflections on the evolution of migration. Pages 17-31 *in* E.J. Milner-Gulland, J.M. Fryxell and A.R.E. Sinclair, eds. Animal Migrations: A Synthesis. Oxford University Press. Oxford, UK.

Holt, A.J., K.J. Gaston and F. He. 2002. Occupancy-abundance relationships and spatial distribution: A review. Basic and Applied Ecology 3:1-11.

Hooper, H.L., R. Connono, A. Callaghan, G. Fryer, S. Yarwood-Buchanan, J. Biggs, et al. 2008. The ecological niche of *Daphnia magna* characterized using population growth rate. Ecology 89:1015-1022.

Horgan, J. 1991. "Profile: Physicist John A. Wheeler, Questioning the 'It from Bit'". Scientific American 6:36-37.

Huffaker, C.B. 1958. Experimental studies on predation: Dispersion factors and predator-prey oscillations. Hilgardia 27:343-383.

Hurlbert, S.H. 1981. A gentle depilation of the niche: Dicean resource sets in resource hyperspace. Evolutionary Theory 5:177-184.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? American Naturalist 93:145-159.

Hutchinson, G.E. 1978. An Introduction to Population Ecology. Yale University Press, New Haven, CT.

Jagers, P. 1992. Stabilities and instabilities in population dynamics. Journal of Applied Probability 29:770-780.

Jansen, V.A.A. and J. Yoshimura. 1998. Populations can persist in an environment consisting of sink habitats only. Proceedings of the National Academy of Sciences 95:3606-3698.

Jeltsch, F., V. Grimm, J. Reeg and U.E. Schlagel. 2019. Give chance a chance: from coexistence to coviability in biodiversity theory. Ecosphere 10:1-19, e02700.

Kaplan, J. 2008. The end of the Adaptive Landscape metaphor? Biology and Philosophy 23:625-638.

Keddy, P.A. 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. Oecologia 52:348-355.

Keitt, T.H., M.A. Lewis and R.D. Holt. 2001. Allee effects, invasion pinning, and species' borders. American Naturalist 157: 203-216.

Kendall, D.G. 1948. On the generalized "birth-and-death" process. Annals of Mathematical Statistics 19:1-15.

Klein, D.R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32:350–367.

Kokko, H., A. Chaturvedi, D. Croll, MC. Fischer, F. Guillaume and S. Karrenberg. 2017. Can evolution supply what ecology demands? Trends in Ecology and Evolution 32:187-197.

Kortessis, N. and R.D. Holt ms. Scale transition theory as a tool for parsing out dynamics in fragmented landscapes.

Kortessis, N., M.W. Simon, M. Barfield, G.E. Glass, B.H. Singer and R.D. Holt. 2020. The interplay of movement and spatiotemporal variation in transmission degrades pandemic control. Proceedings of the National Academy of Sciences of the USA 117:30104-30106.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314-334.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142:911-927.

Lande, R. 1998. Demographic stochasticity and Allee effect on a scale with isotrophic noise. Oikos 76:5-13.

Lande, R., S. Engen, and B.-E. Saether. 2003. Stochastic Population Dynamics in Ecology and Conservation. Oxford University Press.

Lande, R. and S.H. Orzack. 1988. Extinction dynamics of age-structure populations in a fluctuating environment. Proceedings of the National Academy of Sciences 85:7418-7421.

Laughlin, D.C., J.R. Gremer, P.B. Adler, R.M. Mitchell and M.M. Moore. 2020. The net effect of functional traits on fitness. Trends in Ecology and Evolution 35:1037-1047.

Lawrence, J.P., B. Rojas, A. Fouquet, J. Mappes, A. Blanchette, R.A. Saporito, R. J. Bosque, E.A. Courtois, and E.P. Noonan. 2019. Weak warning signals can persist in the absence of gene flow. Proceedings of the National Academy of Science 116:19037-19045.

Lechowicz, M.J. and G. Bell. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. The Journal of Ecology 687-696.

Leibold, M.A. 1995. The niche concept revisited: Mechanistic models and community context. Ecology 76:1371-1382.

Leigh, E.G., Jr. 1981. The average lifetime of a population in a varying environment. Journal of Theoretical Biology 90:213-239.

Levins, R. 1979. Coexistence in a variable environment. American Naturalist 114:765-783.

Lewontin, R.C. 1963. Models, mathematics and metaphors. Synthese 15:222-244.

Lewontin, R.C. and D. Cohen. 1969. On population growth in a randomly varying environment. Proceedings of the National Academy of Sciences 62: 1056-1060.

Lewontin, R.D. and M.J. D. White. 1960. Interaction between inversion polymorphisms of two chromosome pairs in the grasshopper, Moraba scurra. Evolution 14: 116-229.

Lion, S. and J.A.J. Metz. 2018. Beyond R_0 maximisation: On pathogen evolution and environmental dimensions. Trends in Ecology and Evolution 33:458-473.

Loreau, M., T. Daufresne, A. Gonzalz, D. Gravel, F. Guichard, S.J. Leroux, et al. 2013. Unifying sources and sinks in ecology and Earth sciences. Biological Reviews 88:365-379.

Ludwig, G. 1996. The distribution of population survival times. American Naturalist 147:506-526.

MacArthur, R.H. 1972. Geographical Ecology. Harper & Row, New York, NY.

MacArthur, R.H. and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Maguire, B., Jr. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. American Naturalist 107:213-246.

Martinez-Meyer, E., D. Diaz-Porras, A.T. Peterson and C. Yanez-Arenas. 2013. Ecological niche structure and rangewide abundance patterns of species. Biology Letters 9:20120637.

Matthew D.P. and A. Gonzalez. 2007. The inflationary effect of environmental fluctuations ensure the persistence of sink metapopulations. Ecology 88:2848-2856.

Matthiopoulus, J. 2021. How animals endure by bending environmental space: Redefining the fundamental niche. bioRxiv preprint doi: https://doi.org/10.1101/2021.02.01.429132

Maynard-Smith, J. 1989. Evolutionary Genetics. 1st edition, Oxford University Press. Oxford, UK.

McCoy, M.W., M. Barfield and R.D. Holt. 2009. Predator shadows: Complex life histories as generators of spatially patterned indirect interactions across ecosystems. Oikos 118: 87-100.

McGill, B.J. 2012. Trees are rarely most abundant where they grow best. Journal of Plant Ecology 5:46-51.

McInerny, 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 39:2096-2102.

McInerny, G.J. and R.S. Etienner. 2012b. Stitch the niche – a practical philosophy and visual schematic for the niche concept. Journal of Biogeography 39:2103-2111.

McPeek, M.A. 2017. Evolutionary Community Ecology. Princeton University Press, Princeton, New Jersey.

Merow, C., A.M. Latimer, A.M. Wilson, S.M. McMahon, A.G. Rebelo and J.A. Silander, Jr. 2014. On using integral projection models to generate demographically driven predictions of species' distributions: development and validation using sparse data. Ecography 17:1167-1183.

Meszéna, G., M. Gyllenberg, L. Pásztor, and J. A.J. Metz. 2006. Competitive exclusion and limiting similarity: a unified theory. Theoretical Population Biology 69:68-87.

Metcalf, C.J.E. and S. Pavard. 2007. Why evolutionary biologists should be demographers. Trends in Ecology and Evolution 22:205-212.

Metz, J.A.J. 2014. Fitness, Reference Module in Earth Systems and Environmental Sciences, Elsevier.

Metz, J.A.J., R.M. Nisbet and S.A.H. Geritz. 1992. How should we define 'fitness' for general ecological scenarios. Trends in Ecology and Evolution 7:198-202.

Mordecai, E.A., J.M. Caldwell, M.K. Grossman, C.A. Lippi, L.R. Johnson, M. Neira, et al. 2019. Thermal biology of mosquito-borne disease. Ecology Letters 22:1690-1708.

Nathan, R., W.M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz and P.E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105:19052-19059.

Normand, S., N.E. Zimmermann, F.M. Schurr and H. Lischke. 2014. Demography as the basis for understanding and predicting range dynamics. Ecography 37:1149-1154.

Nunan, N., H. Schmidt, and X. Raynaud. 2020. The ecology of heterogeneity: soil bacterial communities and C dynamics. Philosophical Transactions of the Royal Society, B 375: 20120190249

Nunney L. 1999. Lineage selection: natural selection for long-term benefit. Pages 238-252 *in* L. Keller, Ed Levels of selection in evolution. Princeton University Press. Princeton, New Jersey.

Oldfather, M.F., M.M. Kling, S.N. Sheth, N.C. Emery, and D.D. Ackerly. 2019. Range edges in heterogeneous landscapes: Integrating geographical scale and climate complexity into range dynamics. Global Change Biology 26:1055-1067.

Olson, M.E., A. Arroyo-Santos, and F. Vergara-Silva. 2019. A user's guide to metaphors in ecology and evolution. Trends in Ecology and Evolution 34:605-615.

Orr, H.A. 2007. Absolute fitness, relative fitness, and utility. Evolution 61:2997-3000.

Orr, H.A. 2009. Fitness and its role in evolutionary genetics. Nature Review Genetics 10:531-539.

Osorio-Olvera, J. Soberon and M. Falconi. 2019. On population abundance and niche structure. Ecography 42:1415-1425.

Osorio-Olvera, L., C. Yalez-Arenas, E. Martinez-Mery and A.T. Peterson. 2020. Relationships between population densities and niche-centroid distances in North American birds. Ecology Letters 23:555-564.

Orzack, S.H. 1993. Life history evolution and population dynamics in variable environments: Some insights from stochastic demography. Pages 63-104 *in* J. Yoshimura and C.W. Clark, eds., Adaptation in Stochastic Environments. Lecture Notes in Biomathematics. Springer-Verlag. Berlin, Germany.

Orzack, S.H. 1997. Life history evolution and extinction. Pages 273-302 *in* S. Tuljapurkar and H. Caswell, eds. Structured-Population Models in Marine, Terrestrial, and Freshwaters Systems. Chapman & Hall, UK.

Ovaskainen, O. and B. Meerson. 2010. Stochastic models of population extinction. Trends in Ecology and Evolution 25:643-652.

Ovaskainen, O., H.J. de Knegt, and M. del Mar Delgado. 2016. Quantitative Ecology and Evolutionary Biology: Integrating Models with Data. Oxford University Press, Oxford, UK.

Ovaskainen, O., P. Somervuo and D. Finkelshtein. 2021. Mathematical and simulation methods for deriving extinction thresholds in spatial and stochastic models of interacting agents. Methods in Ecology and Evolution 12:162-129.

Pagel, J., M. Treurnicht, W.J. Bond, T. Kraaij, H. Nottebrock, A. Schutte-Vlok, et al. 2020. Mismatches between demographic niche and geographic distributions are strongest in poorly dispersed and highly persistent plant species. Proceedings of the National Academy of Sciences 117:3663-3669.

Pande, J. T. Fung, R. Chisholm, and N. M. Shnerb. 2020. Mean growth rate when rare is not a reliable metric for persistence of species. Ecology Letters 23:274-282.

Pásztor, L., G. Meszéna, and E. Kisdi. 1996. R_0 or r: A matter of taste? Journal of Evolutionary Biology 9:511-518.

Pásztor, L., Z. Botta-Dukát, G. Magyar, T. Czárán, and G. Meszéna. 2016. Theory -based Ecology: A Darwinian Approach. Oxford University Press. Oxford, UK.

Peay, K.F. 2016. The mutualistic niche: Mycorrhizal symbiosis and community dynamics. Annual Review of Ecology, Evolution and Systematics 47:143-164.

Pedruski, M.T., G.F. Fussmann, and A. Gonzalez. 2015. Predicting the outcome of competition when fitness inequality is variable. Proceedings of the Royal Society, Interface 2:150475.

Pedruski, M.T., G.P. Fussmann and A. Gonzalez. 2016. A network approach reveals surprises about the history of the niche. Ecosphere 7(3):e10266.

Pence, C.H. and G. Ramsey. 2015. Is organismic fitness at the basis of evolutionary theory? Philosophy of Science 82:1081-1091.

Peterson, A.T., J. Soberón, R.G. Pearson, R.P. Anderson, E. Martinez-Meyer, M. Nakamura and M. B. Araujo. 2011. Ecological Niches and Geographical Distributions. Princeton University Press, Princeton, New Jersey.

Petraitis, P. 2013. Multiple Stable States in Natural Ecosystems. Oxford University Press, Oxford, UK.

Pigliucci, M. 2012. Landscapes, surfaces, and morphospaces: what are they good for? Pages 26-38 *in* Svensson, E.I. and R. Calsbeek, eds. The Adaptive Landscape in Evolutionary Biology. Oxford University Press. Oxford, UK.

Pironen, S., G. Papuga, J. Villellas, A.L. Angert, M.B. Garcia and J.D. Thompson. 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm. Biological Reviews 92:1877-1909.

Pironen, S., J. Villellas, W. Thuiller, V.M. Eckhart, M.A. Geber, D.A. Moeller and M. B. Garcia. 2018. The 'Hutchinsonian niche' as an assemblage of demographic niches: implications for species geographic ranges. Ecology 41:1103-1113.

Pulliam, H.R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349-261.

Pulliam J.R., J.G. Dushoff, S.A. Levin, and A.P.Dobson. 2007 Epidemic enhancement in partially immune populations. PLoS ONE 2(1): e165. https://doi.org/10.1371/journal.pone.0000165.

Queller, D.C. 2020. The gene's eye view, the Gouldian know, Fisherian swords and the causes of selection. Phil. Trans.R. Soc. B 375:20190354.

Ramsey, G. and C.H. Pence. 2013. "Fitness: philosophical problems." In *eLS.* Chichester: John Wiley & Sons, Ltd.. Chichester, UK. doi: 10.1002/9780470015902.a0003443.pub2.

Renshaw, E. 2013. Stochastic Population Processes. Oxford University Press.

Resetarits, W.J., Jr., M.R. Pintar, J.R. Bohenek, and T.M. Breech. 2019. Patch size as a niche dimension: aquatic insects behaviorally partition enemy-free space across gradients of patch size. American Naturalist 194:776-793.

Rice, S.H. 2004. Evolutionary Theory: Mathematical and Conceptual Foundations. Sinauer, Sunderland, MA.

Richard, M., T. Bernhardt, and G. Bell. 2000. Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest. Ecography 23:231-245.

Roff, D.A. 2008. Defining fitness in evolutionary models. Journal of Genetics 87:339-348.

Rosales, A. 2017. Theories that narrate the world: Ronald A. Fisher's mass selection and Sewall Wright's shifting balance. Studies in History and Philosophy of Science 62:22-30.

Rousset, F. 2004. Genetic Structure and Selection in Subdivided Populations. Princeton University Press. Princeton, New Jersey.

Roy, M., R.D. Holt and M. Barfield. 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. American Naturalist 166: 246-261.

Royama, T. 1992. Analytical Population Dynamics. Chapman & Hall, London, UK.

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 11o:103701.

Santini, L., S. Pironon, L. Maiorano and W. Thuiller. 2019. Addressing common pitfalls does not provide more support to geographical and ecological abundant-centre hypotheses. Ecography 42:696-705.

Sax, D.F., R. Early and J. Bellemeare. 2013. Niche syndromes, species extinction risks, and management under climate change. Trends in Ecology and Evolution 28:517-523.

Scheffers, B.R., D.P. Edwards, S.L. Macdonald, R.A. Senior, L.r. Andriamahohatra et al. 2017. Extreme thermal heterogeneity in structurally complex tropical rain forests. Biotropica 49:35-44.

Schmidt, K.A. 2004. Site fidelity in temporally correlated environments enhances population persistence. Ecology Letters 7:176-184.

Schmidt, K.A., F. Massol. 2019. Habitat selection and the value of information in heterogeneous landscapes. Oikos 128:457-467.

Schoener, T.W. 1989. The ecological niche. Pages 29-113 *in* J.M. Cherrett, ed. Ecological Concepts. Blackwell, Oxford.

Schreiber, S.J., J.M. Levine, O. Godoy, N.J.B. Kraft and S.P. Hart. 2020. Does deterministic coexistence theory matter in a finite world? Insights from serpentine annual plants. bioRxiv doi: https://doi.org/10.1101/290882

Schurr, F.M., J. Pagel, J.S. Cabral, J. Groeneveld, O. Bykova, R.B. O'Hara, et al. 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. Journal of Biogeography 39:2146-2162.

Silvertown, J. 2016. Ecologists need to be cautious about economic metaphors: a reply. Trends in Ecology and Evolution 31:336.

Simpson. G.G. 1944. Tempo and Mode in Evolution.Columbia University Press, New York, NY. (reprinted 1989, Columbia Classics).

Skipper, R.A. Jr. and M.R. Dietrich. 2012. Sewall Wright's adaptive landscape: Philosophical reflections on heuristic value. Pages 16-25 *in* E.I. Svensson and R. Calsbeek, eds. The Adaptive Landscape in Evolutionary Biology. Oxford University Press. Oxford, UK.

Snyder, R.E. and P. Chesson. 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. American Naturalist 164:633-650.

Sober, E. 2001. The two faces of fitness. Pages 309-321 *in* R. Singh, D. Paul,C. Krimbas, and J. Beatty eds., Thinking about Evolution: Historical, Philosophical, and Political Perspectives. Cambridge University Press, Cambridge, UK.

Soberón, J. 2010. Niche and area of distribution modeling: A population ecology perspective. Ecography 33:159-167.

Soberón, J., A.T. Peterson. 2020. What is the shape of the fundamental Grinnellian niche? Theoretical Ecology 13:105-115.

Spencer H.G. 2020. Beyond equilibria: The neglected role of history in ecology and evolutionary biology. Quarterly Review of Biology 95:311-321.

Stocker, R. and J.R. Seymour. 2012. Ecology and physics of bacterial chemotaxis in the ocean. Microbiology and Molecular Biology Reviews 76:792–812.

Svensson, E.I. and R. Calsbeek, eds. 2012. The Adaptive Landscape in Evolutionary Biology. Oxford University Press. Oxford, UK.

Thuiller, W., T. Munkemuller, K.H. Schiffers, D. Georges, S. Dullinger, V.M. Eckhart, et al. 2014. Does probability of occurrence relate to population dynamics? Ecography 38:221-230.

Treurnicht, M., J. Pagel, K.J. Esler, A.L. Schutte-Viok, H. Nottebrock, T. Kraaij, et al. 2016. Environmental drivers of demographic variation across the global geographical range of 26 plant species. Journal of Ecology 104:331-342.

Treurnicht, M., J. Pagel, J. Tonnabel, K.J. Esler, J.A. Slingsby, and F.M. Schurr. 2020. Functional traits explain the Hutchinsonian niches of plant species. Global Ecology and Biogeography 29:534-545.

Villellas,J., D.F. Doak, M.B. Garcia and W.F. Morris. 2015. Demographic compensation among populations: what is it, how does it arise and what are its implications? Ecology Letters 18: 1139-1152.

Vincent, T.L. and J.S. Brown. 2005. Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics. Cambridge University Press, Cambridge, UK.

Voje, K.L. 2020. Testing eco-evolutionary predictions using fossil data: Phyletic evolution following ecological opportunity. Evolution 74: 188-200.

Wade, M.J. 2012. Wright's adaptive landscape: Testing the predictions of his shifting balance theory. pp. 58-73 *in* E.I. Svensson and R. Calsbeek, eds. The Adaptive Landscape in Evolutionary Biology. Oxford University Press. Oxford, UK.

Whittaker, R.H. and S.A. Levin. 1975. Niche: Theory and Application. Benchmark Papers in Ecology, Vol. 3. Dowden, Hutchinson & Ross, Stroudsberg, PA.

Whittaker, R.H., S.A. Levin, and R.B. Root. 1973. Niche, habitat, and ecotope. The American Naturalist 107:321-338.

Wiens, J.J., D.D.Ackerly, A.P. Allen, B.L. Anacker, L.B. Buckley, H.V. Cornell, E.I. Damschen, T.J. Davies, J-A. Grytnes, S.P. Harrison, B.A. Hawkins, R.D. Holt, C.M. McCain, and P.R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters 13: 1310-1324.

Wright, S. 1932. The roles of mutation, inbreeding, cross-breeding and selection in evolution. In D.F. Jones, Ed., Proceedings of the Sixth Annual Congress of Genetics. 1:356-366. Reprinted in W.B. Provine. 1966. Sewall Wright: Evolution: Selected Papers. University of Chicago Press, Chicago, IL. pp. 161-177.

Wright, S. 1942. Statistical genetics and evolution. Bulletin of the American Mathematical Society 48:223-246.

Wright, S. 1959. Physiological genetics, ecology of populations, and natural selection. Perspectives in Biology and Medicine 3:107-151.

Wright, S. 1988. Surfaces of selective value revisited. American Naturalist 131:115-123.

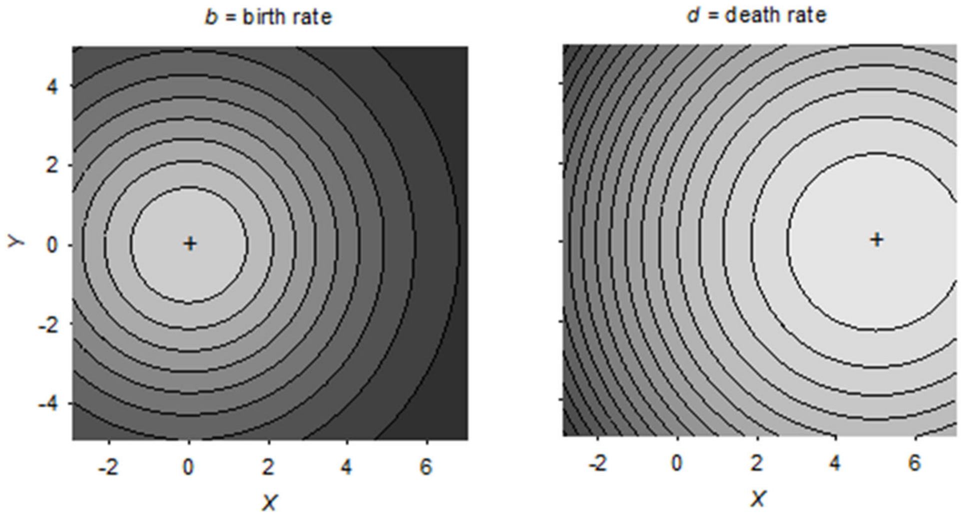


Figure 1. A schematic example of vital rates as a function of two abstract environmental variables, X and Y. On the left, birth rate is represented as a Gaussian, centered at (0,0), with “width” of sqrt(10) in all directions, so $b = 10 \exp\{-(X^2 + Y^2)/20\}$; inner contour is $b = 9$, spacing is 1. On the right, the death rate is parabolic with a minimum = 1 at (5,0), with quadratic coefficient = 0.2, so $d = 1 + 0.2[(X - 5)^2 + Y^2]$; inner contour is 2, spacing is 1. Lighter shades indicate “better” environments (e.g., higher births, lower deaths). The optimal environment for birth differs from that for death (both indicated with a cross).

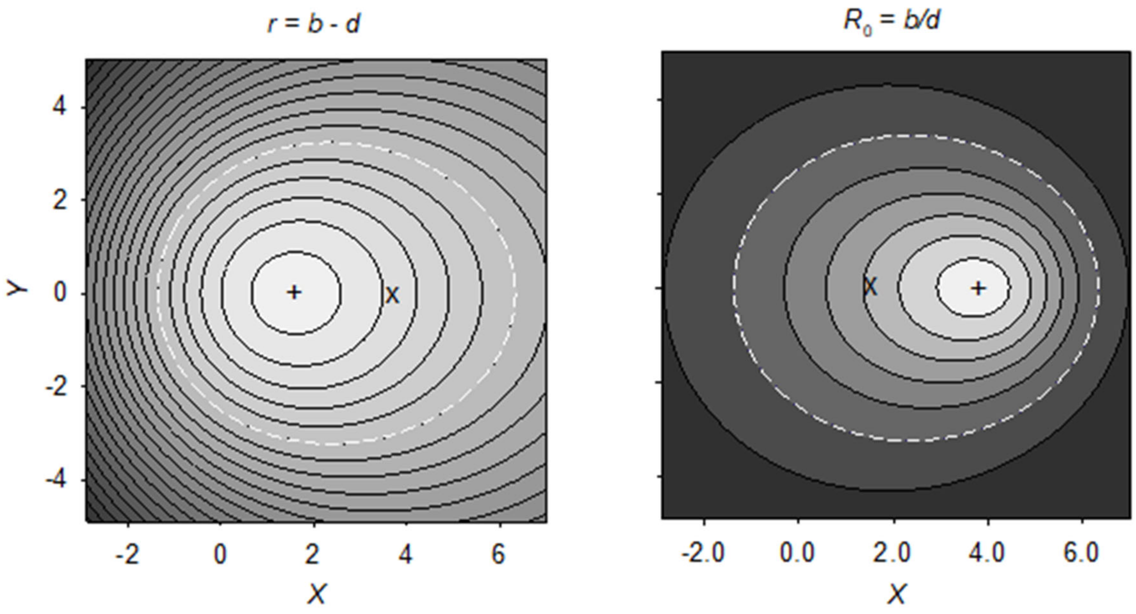


Figure 2. The Hutchinsonian niche, constructed using two different fitness metrics computed from the same environmental dependencies of vital rates. Lighter shading denotes higher fitness. Left panel, a niche response surface constructed with Intrinsic growth rates ($r = b - d$), using the vital rate patterns depicted in figure 1. Right panel shows a niche response surface based on lifetime reproductive success ($R = b/d$), with the same vital rates. In both cases, the dashed white oval is the niche boundary where populations are in deterministic equilibrium; this niche boundary is the same for the two metrics. However, away from equilibrium, the two metrics diverge. The black plus signs mark the optimal environment for each metric; the black crosses indicate the optimal environments, for the other metric. The optima differ, as do the shapes of the two niche response surfaces (r is has a steeper slope to the left, whereas R is steeper to the right).

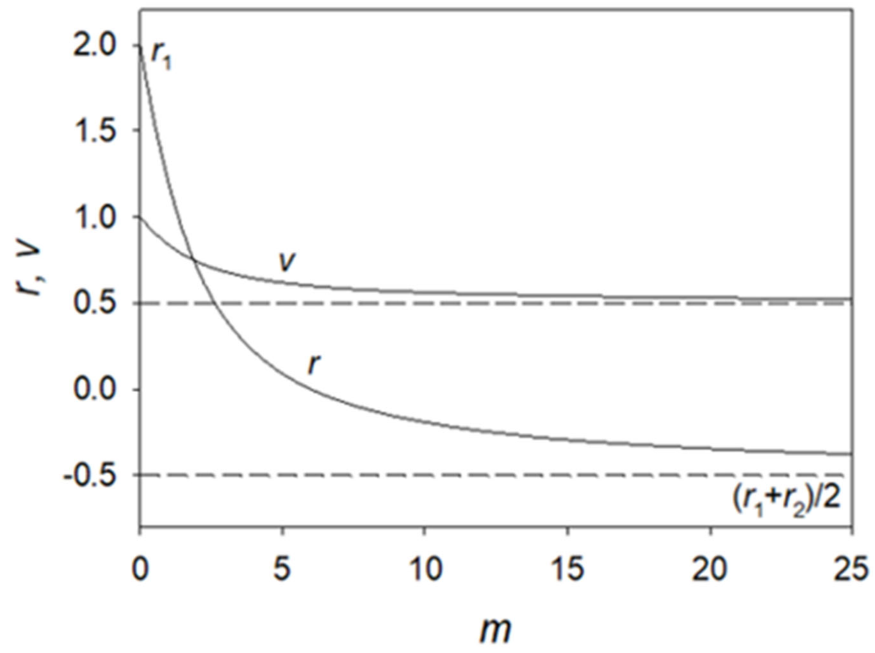


Figure 3: Low rates of dispersal imply positive covariance between local abundances and growth rates. Two habitats of equal area are connected symmetrically by passive dispersal, Abundances are sufficiently low to ignore density dependence. Population dynamics are described by $dN_1 / dt = r_1 N_1 - mN_1 + mN_2$, $dN_2 / dt = r_2 N_2 - mN_2 + mN_1$, where N_i and r_i are respectively abundances and intrinsic rate of increase in habitat *i*, and *m* is a rate of movement. The asymptotic growth rate of the whole population is *r*. The stable patch distribution is *v* (= $N_1/(N_1+N_2)$), the fraction of the population in habitat 1. In the example $r_1 = 2$, $r_2 = -3$. At high *m*, the growth rate is the spatial average of the *r*s, which is negative. At lower *m*, the asymptotic growth rate increases, because relatively more individuals reside in the better habitat.

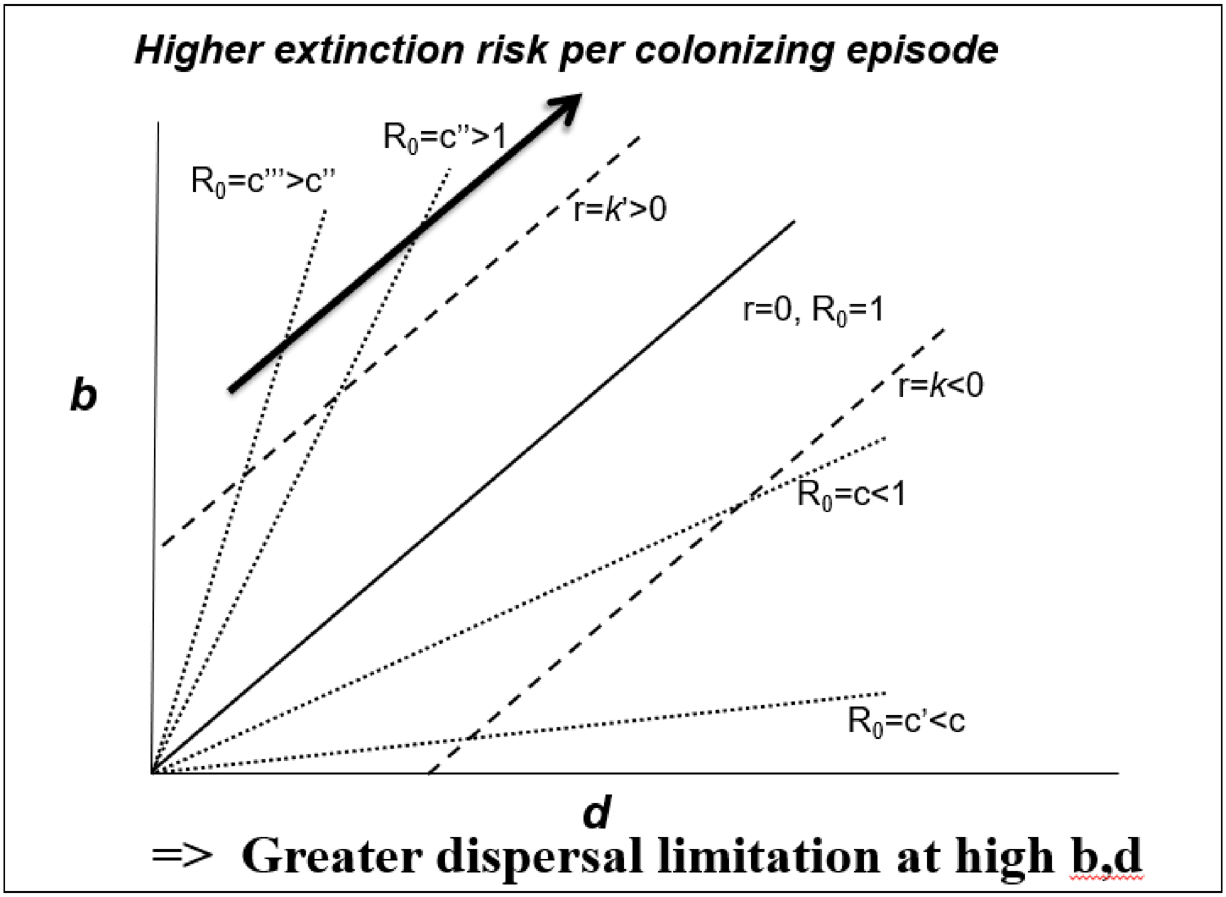
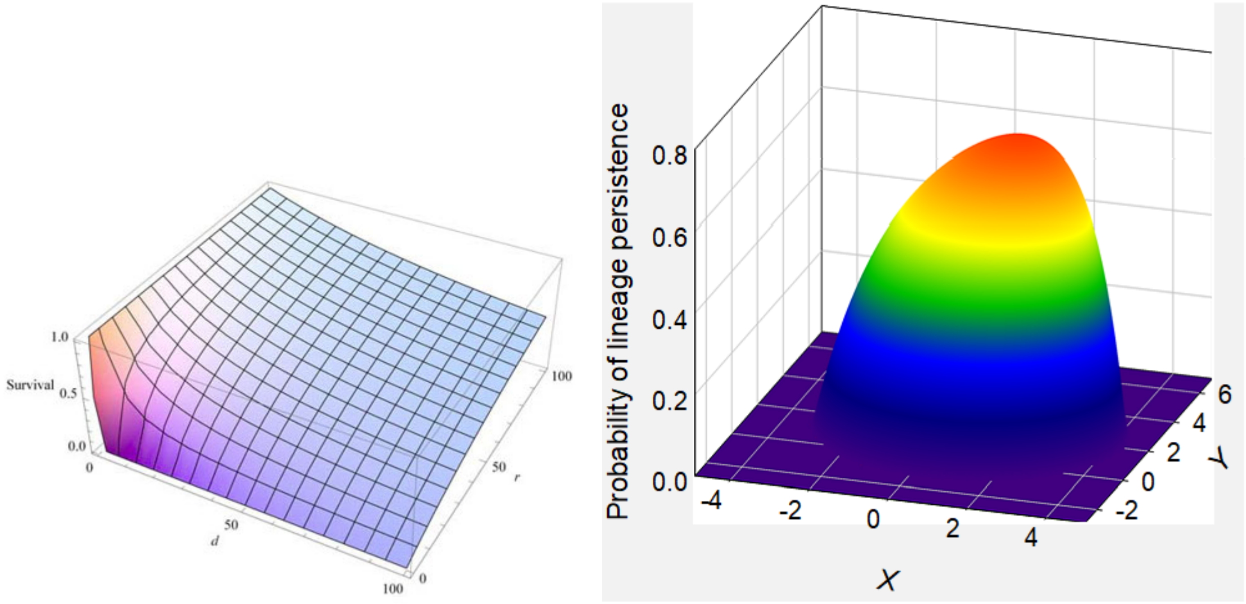


Figure 4. Alternative fitness metrics, constructed from the basic vital rates for unstructured populations: birth and death rates (exponential growth or decline in a constant environment). In the *b*-*d* plane, the intrinsic growth rate $r = b - d$ defines a family of parallel lines of slope 1, whereas lifetime reproduction $R = b/d$ defines a family of lines that all emanate from the origin. The two family of lines coincide for populations in equilibrium, but not for populations that are either growing or declining. Using the argument presented in the main text for long-term persistence of a clonal species, for clones with equivalent *r*s, those with higher *d*s are more likely to suffer extinction, and so more likely to be absent in habitats within their Hutchinsonian niche (as traditionally defined), if dispersal opportunities are limited.



A. B.

Figure 5. Probability of lineage survival or persistence, using the 1948 Kendall model. A single clonal colonist has been introduced into a habitat, and its fate is followed. A. Probability its lineage survives, as a function of death rate *d*, and intrinsic growth rate, *r*. For any given $r > 0$ (the lines of slope 1 in fig. 5), the probability of lineage survival declines with increasing *d*. As *d* increases, the benefit of increasing *r* on lineage survival is diminished. B. Using the hypothetical birth and death rates as a function of environmental variables *X* and *Y* of Figure 1, leading to the *R*-profile of figure 2, implies the surface of the probability of persistence shown here. The environment where persistence probability is optimized differs from the one where the intrinsic growth rate is greatest.

Online Appendix

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Initial conditions and probability of persistence

Appendix A: Introduction

In deterministic treatments of the niche expressed as a response surface of intrinsic growth rate as a function of environmental variables, initial conditions often fade away. For instance, in an age-structured population without density dependence, the asymptotic growth rate of the population does not depend upon its initial age structure. This does not hold, given demographic stochasticity. In this Appendix, we show for two simple examples of population structure (juveniles and adults, and two habitats coupled by dispersal), that initial conditions influence the probability of persistence, even in the absence of density dependence. We use a branching process approach to illustrate this basic point.

With no density dependence and clonal reproduction, the fate of a population (e.g., extinction versus persistence) can be analyzed in terms of the fates of lineages starting from each individual in the initial population. If the focal organism (or variety) is rare, demographic stochasticity is important, and branching process analyses include the effects of this stochasticity. Density dependence for organisms that are rare during colonization is usually not important (unless there are Allee effects), and branching process analyses usually assume no density dependence. The use of branching processes to determine probability of extinction for a real population assumes that by the time the lineage of the initial individual is large enough for density dependence to be important, it is large enough that extinction due to demographic stochasticity is very unlikely. Branching processes in effect give the probability of entering this state.

Branching processes have many applications in ecology, particularly in organisms with clonal growth and in systems in which density dependence can be ignored (for example, when the focal organism is rare). The basic mathematical approach is laid out in fine textbooks in applied mathematics (e.g., Hacccou et al. 2005; Renshaw 2013), but it is useful to walk through the basic approach before we get to specific examples, so as to define some basic terms and introduce useful notation.

Branching processes are often analyzed using probability generating functions (PGFs), which are functions of the probability distribution of one or more discrete random variables (representing individuals). For example, a PGF can be defined representing the probability distribution of the number of offspring of an individual (or, more generally, the number of individuals at one time that result from one individual at a previous time) as a power series, in effect an alternative representation of that distribution. If there is only one type of individual, this PGF is given by

$$f_{t+\Delta t}(s) = \sum_{j=0}^{\infty} p_t(j) s^j \,, \tag{A1}$$

where $p_t(j)$ is the probability that one individual at the current time (t) gives rise to j individuals at the next time ($t + \Delta t$; p_t can include the parent as well as offspring if generations are overlapping). If the probabilities are independent of time, the subscripts are generally omitted. For example, in some cases the number of offspring can be assumed to follow a Poisson distribution with mean R, in which case $p(j) = \exp\{-R\} R^j / j!$ (assuming discrete generations, so the parent reproduces and dies, leaving only its offspring). Substituting this into (A1) gives

$$f(s) = e^{-R} \sum_{j=0}^{\infty} \frac{(Rs)^j}{j!} = e^{R(s-1)} \,. \tag{A2}$$

If there are overlapping generations, then $p(j)$ should include the parent, in which case $p(0)$ is the probability that there are no offspring and the parent dies, $p(1)$ is the probability that there is one offspring and the parent dies, or there are no offspring and the parent survives (since both these result in one individual at the next time), etc.

The PGF for a population can be defined using an equation analogous to equation (A1):

$$F_t(s) = \sum_{j=0}^{\infty} P_t(j) s^j \,, \tag{A3}$$

where $P_t(j)$ is the probability that there are j individuals in the population at time t.

If all individuals are assumed to be the same and their parameters do not change with time, then eventually the probability of extinction of a population initiated by a single individual at time 0 will change very little with time (because after a long time the population either has gone extinct or become large enough that it is very unlikely to go extinct in the future). If q_t is the probability that the population is extinct at time t, then the probability that it is extinct at time $t + \Delta t$ can be written in terms of q_t and the number of individuals at time Δt (assuming one individual at time 0, and so counting at time Δt later), using $q_{t+\Delta t} = \sum_j \Pr(A_j)\Pr(E_{t+\Delta t}|A_j)$ where Pr(X) is the probability of event X, $E_{t+\Delta t}$ is extinction at time $t + \Delta t$, and A_j is the event that there are j individuals at time Δt. (For a discrete-time models, Δt is often set to 1, while for continuous-time models, it is often set to an infinitesimal interval dt.) If there were no individuals at time Δt, which happens if the initial individual dies without reproducing [and has probability $P_{\Delta t}(0)$], the population is extinct at that and all subsequent times, so $q_{t+\Delta t} = 0$. If there was 1 individual at time Δt [probability $P_{\Delta t}(1)$], then $q_{t+\Delta t} = q_t$ (since in this case we have one individual at time Δt, and the probability that its lineage survives to time $t + \Delta t$ is the same as the probability that the lineage of one individual at time 0 survives until time t). If there were 2 individuals at time Δt [probability $P_{\Delta t}(2)$], for example if the initial individual produces two offspring and dies in the initial interval, then $q_{t+\Delta t} = q_t^2$, since there will be 2 individuals at time Δt and the lineages of both must go extinct for the population to go extinct. Extinctions of the two lineages are independent and each equal to q_t. The probability of lineages of n offspring going extinct is similarly q_t^n, so this is $q_{t+\Delta t}$ given n individuals at time Δt. Summing these values weighted by the probability of each number of individuals at time Δt gives

$$q_{t+\Delta t} = P_{\Delta t}(0) + P_{\Delta t}(1)q_t + P_{\Delta t}(2)q_t^2 + P_{\Delta t}(3)q_t^3 + \cdots = \sum_{j=0}^{\infty} P_{\Delta t}(j)q_t^j = F_{\Delta t}(q_t), \tag{A4}$$

in which the last step uses the definition of the PGF in equation (A3). $F_{\Delta t}(s)$ is the PGF for the number of individuals at time Δt that result from a single individual at time 0. Therefore, it is equivalent to $f(s)$

defined in equation (A1) (time independence has been assumed, so no subscript is needed). Since the probability of extinction eventually becomes almost constant, then for a sufficiently large time $q_{t+\Delta t} = q_t = q$ in equation (A4), which gives an equation for probability of extinction, called a fixed point equation, for this scenario:

$$q = f(q). \tag{A5}$$

There is always a solution to (A5) at $q = 1$. The probability of extinction is less than 1 only if there is a solution to (A5) that is less than 1 (and nonnegative).

Equation (A5) assumes that conditions do not change over time. If this is not the case, then the probability of extinction can still be found. The population is generally started with one individual, so initially for the population $P_0(1) = 1$ and $P_0(j) = 0$ for all other j (the population size is 1 with probability 1), making $F_0(s) = s$. For discrete-time models, the population PGF at time $t + 1$ is found from its PGF at time t by substituting $f_{t+1}(s)$, the PGF for individuals produced in generation (or time step) $t + 1$, for s in the population PGF, so $F_{t+1}(s) = F_t(f_{t+1}(s))$. This recursion can be used to find the probability of extinction at generation t, which is $F_t(0)$ [taking the limit as s approaches 0 in (A3) gives $P_t(0)$, the probability that there are no individuals at generation t]. Generally, a numerical solution is required.

If the population consists of n types of individuals, then an n-type branching process is used. In this case, there is a PGF for each type i of individual:

$$f_i(s_1, s_2, \ldots, s_n) = \sum_{j,k,\ldots,l=0}^{\infty} p_i(j,k,\ldots,l) s_1^j s_2^k \cdots s_n^l; \qquad i = 1, n, \tag{A6}$$

where now $p_i(j,k,\ldots,l)$ is the probability that one type-i individual gives rise to j type-1 individuals, k type-2 individuals, … , and l type-n individuals. (This assumes that probabilities are independent of time, and the subscript here is the individual type. If the probabilities change with time, a second subscript for time can be included.) Assuming that the probabilities (p_i) are constant, there are n fixed point equations,

$$q_i = f_i(q_1, q_2, \ldots, q_n); \qquad i = 1, n, \tag{A7}$$

which can be solved for q_i, which is the probability of extinction of a population starting with one individual of type i. This set of fixed point equations is the basis of many of the results presented below.

The different types for an n-type branching process can be different stages (in which case p_i can include elements of the transition matrix), individuals in different habitats, or with different genotypes (such as wild types and mutants, in which case p_i can include mutation rates).

Single-stage population

We start with the simplest case (a version of the Kendall model used in the main text). An individual can die (at per capita rate d) or give rise to an offspring (per capita rate b). In an infinitesimal time dt, at most one of these events can happen (such as if b and d are Poisson processes). The probability that the initial individual dies is $d\ dt$, the probability that it produces an offspring is $b\ dt$, and the probability that neither happens is $1 - d\ dt - b\ dt$. Therefore $p(0) = d\ dt$ (if the individual dies, there are no individuals), $p(1) = 1 - d\ dt - b\ dt$ (if nothing happens, the one individual remains), and $p(2) = b\ dt$ (offspring production results in two individuals). Plugging these into (A5) (assuming the rates are constant) yields the fixed point equation

$$q = d\ dt + (1 - b\ dt - d\ dt)q + b\ dt\ q^2 . \qquad \text{(A8)}$$

Subtracting q from both sides and dividing by dt gives, $0 = d - (b+d)q + b\ q^2$, the solutions of which are 1 and d/b. If $d > b$, the probability of extinction is 1; otherwise, it is $d/b = 1/R$, where $R = b/d$ is the reproduction number (average number of offspring per adult; new individuals are produced at rate b for the average lifetime $1/d$). Therefore, the probability of persistence is $1 - 1/R$ (eq. [9] in the main text).

If the population instead initially had n individuals, the probability of the population surviving would be the probability that the lineage of any of the founders survived, which would be $1-(d/b)^n$.

Appendix B: Two-stage population

Branching processes can also be used to find the probability of persistence of an initially sparse population consisting of individuals with two stages, juveniles and adults. In a continuous-time model, juveniles grow into adults at a rate of g and die at rate d_1, while adults produce juveniles at rate b and die at rate d_2 (all rates are per capita and temporally constant). Again, we assume that a single clonal individual is introduced. That individual could be either a juvenile or adult. Assuming there is no density dependence (such as when the population is low), the probability of persistence of this population can be analyzed as a two-type branching process, using equation (A7) with $n = 2$ (and using the definition in eq. [A6]); $p_i(j,k)$ is the probability that one type-i individual gives rise to j type-1 individuals (juveniles) and k type-2 individuals (adults).

Because the total probability of all possible events arising from each type individual must be 1, $q_i = 1$ for all i is always a solution of (A7), but there are generally other solutions, which can be feasible ($0 \le q_i \le 1$), or not. If there are no other feasible extinctions, then the probability of extinction is 1. The probabilities $p_i(j,k)$ are calculated over an infinitesimal time interval dt, during which it is assumed that only one event (growth, birth or death) can occur. A juvenile dies with probability d_1dt, resulting in no individuals, so $p_1(0,0) = d_1dt$. The juvenile grows with probability $g\ dt$, producing one adult (and losing the juvenile), so $p_1(0,1) = g\ dt$. The juvenile does neither otherwise, resulting in maintenance of one juvenile, so $p_1(1,0) = 1 - g\ dt - d_1dt$. An adult dies with probability d_2dt, resulting in no individuals, so $p_2(0,0) = d_2dt$, gives birth with probability $b\ dt$, producing one juvenile (and retaining the adult), so $p_2(1,1) = b\ dt$, and does neither otherwise, resulting in maintenance of one adult, so $p_2(1,0) = 1 - b\ dt - d_2dt$. Substituting these into equation (A7) gives

$$q_1 = d_1dt + g\ dt\ q_2 + (1 - g\ dt - d_1dt)q_1 \tag{B1}$$

$$q_2 = d_2dt + b\ dt\ q_1q_2 + (1 - b\ dt - d_2dt)q_2 . \tag{B2}$$

After subtracting q_1 from both sides of the first equation and q_2 from the second and dividing each equation by dt, the result is

$$d_1 + gq_2 - (g + d_1)q_1 = 0 , \tag{B3}$$

$$d_2 + bq_1q_2 - (b + d_2)q_2 = 0 . \tag{B4}$$

Equation (B3) can be solved for

$$q_1 = \frac{d_1 + gq_2}{g + d_1} \tag{B5}$$

which can be substituted into (B4), giving a quadratic equation for q_2, which has solutions $q_2 = 1$ (which gives q_1 also equal to 1) and

$$q_2 = \frac{(g + d_1)d_2}{bg} . \tag{B6}$$

If $(g + d_1)d_2 > bg$, equation (B6) gives $q_2 > 1$, and extinction is certain starting from one adult (and also from one juvenile). If $(g + d_1)d_2 < bg$, equation (B6) gives the probability of extinction starting from a single adult. The reciprocal of q_2 in (B6) is the product of the probability that a juvenile grows to an adult [$g / (g + d_1)$] and the average number of offspring of an adult (b / d_2), which is the birth rate over the average adult lifetime. Therefore, this reciprocal is the average number of adults arising from a single adult, and so is analogous to *R*. Therefore, the probability of persistence of a lineage starting with a single adult is $1 - 1 / R$. Substituting (B6) into equation (B5) gives

$$q_1 = \frac{d_1}{g + d_1} + \frac{d_2}{b} \tag{B7}$$

as the probability of extinction starting from one juvenile (assuming it is less than or equal to 1, which it is if q_2 is). It can easily be shown that the probability of persistence of a juvenile is the product of the probability of persistence of an adult and the probability of survival of a juvenile to the adult stage, the latter of which is $g / (g + d_1)$. Therefore, the probability of persistence starting with a juvenile depends on *g* and d_1 in addition to *R*.

The bottom line of this model (comparing [B6] and [B7]) is that the probability of persistence differs depending upon initial conditions – whether or not the initial colonist is a juvenile, or an adult.

This dependence of persistence on initial conditions does not hold for the comparable deterministic exponential growth model with age structure and overlapping generations.

Appendix C: Two-habitat model

Branching processes can also be used to find the probability of persistence for a species colonizing a landscape of two habitats with movement between them. In habitat i (1 or 2), individuals die at rate d_i and give birth at rate b_i, while they move from habitat i to j at rate m_{ij}. Births and deaths are assumed to be Poisson processes, so over an infinitesimal interval dt, only one event occurs. From a single individual in habitat 1, the results can be no individuals with probability $d_1 dt$ (death), one individual in habitat 2 with probability $m_{12} dt$, two individuals in habitat 1 with probability $b_1 dt$, or one individual in habitat 1 with probability $1 - d_1 dt - m_{12} dt - b_1 dt$ (nothing happens). The same alternatives result for an individual in habitat 2, with the habitat numbers switched. Therefore, the fixed point equations are

$$q_1 = d_1 dt + m_{12} dt\ q_2 + b_1 dt\ q_1^2 + (1 - d_1 dt - m_{12} dt - b_1 dt) q_1 \tag{C1}$$

$$q_2 = d_2 dt + m_{21} dt\ q_1 + b_2 dt\ q_2^2 + (1 - d_2 dt - m_{21} dt - b_2 dt) q_2 . \tag{C2}$$

which simplify to $d_1 + m_{12} q_2 + b_1 q_1^2 - (d_1 + m_{12} + b_1) q_1 = 0$ and $d_2 + m_{21} q_1 + b_2 q_2^2 - (d_2 + m_{21} + b_2) q_2 = 0$. The first can be solved for q_2 and this can then be substituted into the second equation, giving

$$\begin{aligned} &d_2 + m_{21} q_1 + b_2 [\{(d_1 + m_{12} + b_1) q_1 - b_1 q_1^2 - d_1] / m_{12}\}^2 \\ &\quad - (d_2 + m_{21} + b_2)[(d_1 + m_{12} + b_1) q_1 - b_1 q_1^2 - d_1] / m_{12} = 0 \end{aligned} . \tag{C3}$$

This is fourth-order in q_1. One solution is $q_1 = 1$, but factoring out that solution still leaves a cubic equation.

It is useful to consider some limiting cases. First, let $b_1 = b_2 = b$, $d_1 = d_2 = d$, and $m_{12} = m_{21} = m$. In this homogeneous case with symmetric movement, we start with

$d_1 + m_{12}q_2 + b_1q_1^2 - (d_1 + m_{12} + b_1)q_1 = 0$ and $d_2 + m_{21}q_1 + b_2q_2^2 - (d_2 + m_{21} + b_2)q_2 = 0$. After substitution, we can rewrite them both as $d + mq_i + bq_i^2 - (d + m + b)q_i = d + bq_i^2 - (d + b)q_i = 0$. Solving the quadratic equation gives

$$q_i = \frac{d+b}{2b} \pm \sqrt{\left(\frac{d-b}{2b}\right)^2} = \frac{d+b}{2b} \pm \left|\frac{d-b}{2b}\right| = \frac{d}{b} \text{ or } 1 \ .$$

There is only a solution < 1 if $d < b$, in which case $q_i = 1/R$ for both habitats, where $R = b/d$. In this case, it is really just one habitat and the spatial subdivision does not matter, so the probability of persistence is $p = 1 - q = 1 - 1/R$.

Next, let $b_1/ d_1 > 1 > b_2/ d_2$, and allow $m_{12} = m_{21} = m$ to become very small. We surmise there should be two roots, one near some $p > 0$, the other very near 1. As m approaches 0, the two equations each approach $d_i + bq_i^2 - (d_i + b_i)q_i = 0$, the solutions to which are d_i/b_i and 1. For habitat 1, the solution is d_1/b_1, and for habitat 2, it is 1. So introduction fails, if it starts in habitat 2, but colonization might succeed, if it happens to be in habitat 1.

Now, let $m_{12} = m_{21} = m$ get very large. This should approach a well-mixed population, with $b = (b_1 + b_2)/2$, and $d = (d_1 + d_2)/2$. To show this formally, using the equations above, with equal migration rates we have $d_1 + b_1q_1^2 - (d_1 + b_1)q_1 = m(q_1 - q_2) = -[d_2 + b_2q_2^2 - (d_2 + b_2)q_2]$. Since the two outside terms are bounded by the value when q_1 or $q_2 = 1$, as m becomes very large, it is necessary that q_1 approach q_2. Setting them equal to each other (and q) in the outside terms (but note that this does not mean the middle term is 0, since m is becoming very large) gives

$$d_1 + b_1q_1^2 - (d_1 + b_1)q_1 = -[d_2 + b_2q_2^2 - (d_2 + b_2)q_2] \text{ or}$$

$$d_1 + d_2 + (b_1 + b_2)q^2 - (d_1 + d_2 + b_1 + b_2)q = 0 \ .$$

This is of the same form as the equation for the single-stage population, except d and b are replaced by their sums over both habitats. Therefore, both values of q approach $(d_1 + d_2)/(b_1 + b_2)$, which is the same result as it would be if numerator and denominator were half as much (giving d/b).

Possibly more interestingly, we now assume the two habitats differ in their vital rates. Let $b_1/d_1 = R_1$, and $b_2/d_2 = R_2$. What happens when $R_1 = R_2$? The isolated habitat patches would have equivalent probabilities of persistence. Does that hold if say $m_{12} = m_{21}$, or more generally? What happens if the two reproductive ratios differ?

If the R values are the same, then $b_i = Rd_i$ can be substituted into the equations above, giving $d_i + m_{ij}q_j + Rd_iq_i^2 - (d_i + m_{ij} + Rd_i)q_i = 0$ for $i = 1,2$ and $j = 3 - i$. Suppose $q_i = q_j$ (i.e., $q_1 = q_2$). Then the migration terms drop out, giving $d_i + Rd_iq_i^2 - (d_i + Rd_i)q_i = 0$ for $i =1,2$, which has solutions $q_i = 1/R$ for $i =1,2$. This agrees with the assumption that $q_1 = q_2$ and therefore is a solution (which does not require that $m_{12} = m_{21}$). (We do not know if this is the only solution.)

What happens if the intrinsic growth rates r_1 and r_2 are the same, but R_1 does not necessarily equal R_2? Let $b_1 - d_1 = r_1$, $b_2 - d_2 = r_2$. If the R_i values can be different, then if we assume the q_i are equal, we have $d_i + R_id_iq_i^2 - (d_i + R_id_i)q_i = 0$, $i = 1,2$, which has solutions $q_i = 1/R_i$. This is only consistent with the assumption that the q_i are equal ($q_1 = q_2$) if the R_i are equal ($R_1 = R_2$), so this is necessary for q_1 to equal q_2. If the r_i values are equal, the R_i values are not, unless birth rates are equal and deaths rates are equal. So except for this special case (identical habitats), the probability of persistence will depend upon which habitat is first colonized ($q_1 \neq q_2$) if the two habitats have the same intrinsic rate of growth.

There is one technical issue which we should mention, without a completely definitive answer. How many solutions can be between 0 and 1? One argument for at most 1 is based on the observation that the equations for q_i can be written in the form $q_i = [d_j + b_jq_j^2 - (d_j + b_j)q_j]/m_{ji}$. These are parabolas, one concave down and the other to the left. One axis intercept of each is negative, and the parabolas intersect at (1,1). These two parabolas can intersect in at most 4 points, on the upper and lower branch of one and the right and left branch of the other (which will be called the upper and lower branch, because they have higher and lower values of one variable, respectively). If the (1,1) point is on the lower branches, then the other intersections are at values > 1, and the population goes extinct. If it is on the upper branches, then the solution on the lower branches must be between 0 and 1. The other intersections have at least one value > 1 and thus are not feasible solutions. If there are only two intersections and (1,1) is the lower one, the other has a value > 1 and thus is not feasible. If (1,1) is the higher one, then the lower intersection can be a feasible solution. If there are 4 solutions and (1,1) is on one upper and one lower branch, then at most one solution is feasible, since the others have a value > 1. It is also possible that there are two intersections on the lower branch of both parabolas, since they are going in the same direction (up and to the right. In this case, there are no more intersections, and since one of these two is (1,1), there is again at most one feasible solution. We tentatively conclude that there is a unique solution.

The net result of all these machinations is a simple message: the probability of persistence depends upon which habitat is initially colonized, when the habitats have different *R*s. In the juvenile-adult model, it matters which stage is introduced. In other words, because of demographic stochasticity, initial conditions matter when conceptualizing the niche as a surface of probabilities of persistence. As noted in the main text, these effects become less important, the more propagules are introduced, because demographic stochasticity becomes negligible.

Appendix D: Metrics of time to extinction of a continuous-time birth-death process with constant *b* and *d*

The text briefly notes that rather than using probability of persistence as the metric for niche response surfaces, one might use instead an alternative metric such as mean or median time to extinction, say after introduction. Here, we work this suggestion out for the model discussed in the main text. We should note that the model assumes a constant environment, and no density dependence, so these metrics are not finite if growth rates are high. Near the edge of a species' niche, or outside it, growth rates should be low, and these metrics apply to such niche edges (rather than the interior).

For a continuous-time birth-death process with constant per capita birth rate *b* and death rate *d* (births and deaths being Poisson processes), the probability of survival of the lineage of a single individual to time *T* after its birth is

$$P_s = \frac{1-R}{\exp\{-rT\}-R} \ ,$$

where $R = b/d$ is the expected number of offspring per individual and $r = b - d$ is the expected per capita population growth rate, unless $R = 1$, in which case $P_s = 1/(1+bT)$.

Mean time to extinction

The probability of the lineage being extinct at time T is therefore $P_e = 1 - P_s$. This is the probability that the lineage went extinct at or before time T, and therefore is the cumulative distribution function (CDF) of the extinction time. The average time to extinction is

$$E[t_e] = \int_0^\infty T p_e(T)\,dT \ ,$$

where $p_e(T)$ is the probability density function (PDF) of extinction time, which is the derivative of the CDF, dP_e/dT, which is also equal to $-dP_s/dT$ (because $P_e = 1 - P_s$). Therefore,

$$E[t_e] = -\int_0^\infty T(dP_s/dT)\,dT = -\int_{T=0}^\infty T\,dP_s = -TP_s\Big|_0^\infty + \int_0^\infty P_s\,dT = \int_0^\infty P_s\,dT,$$

using integration by parts and assuming that TP_s goes to 0 as T goes to infinity, as is true if $r < 0$ ($R < 1$), which we assume here. Substituting the expression for P_s and integrating gives

$$\begin{aligned}
E[t_e] &= \int_0^\infty \frac{1-R}{\exp\{-rT\}-R}\,dT = (1-R)\left[\frac{T}{-R} - \frac{\ln(\exp\{-rT\}-R)}{rR}\right]_0^\infty \\
&= (1-R)\left[\frac{T}{-R} - \frac{\ln[\exp\{-rT\}(1-R\exp\{rT\})]}{rR}\right]_0^\infty \\
&= (1-R)\left[\frac{T}{-R} - \frac{-rT+\ln(1-R\exp\{rT\})}{rR}\right]_0^\infty = (1-R)\left[-\frac{\ln(1-R\exp\{rT\})}{rR}\right]_0^\infty \\
&= \frac{(1-R)\ln(1-R\ )}{rR}.
\end{aligned}$$

Note that this is a decreasing function of increasing R:

$$\frac{d}{dR}\frac{(1-R)\ln(1-R)}{rR} = \frac{1}{r}\left[\left(\frac{1}{R}-1\right)\frac{-1}{1-R}+\frac{-1}{R^2}\ln(1-R)\right] = \frac{-1}{rR}\left[1+\frac{\ln(1-R)}{R}\right]$$
$$= \frac{-[R+\ln(1-R)]}{rR^2} = \frac{-1}{rR^2}\left[R-\left(R+\frac{R^2}{2}+\frac{R^3}{3}+\cdots+\frac{R^i}{i}+\cdots\right)\right] = \frac{1}{r}\left(\frac{1}{2}+\frac{R}{3}+\cdots+\frac{R^{i-2}}{i}+\cdots\right),$$

which is negative if $r < 0$. It is also a decreasing function of the magnitude of r, as shown in figure 1A (this can easily be shown by differentiating $E[t_e]$ with respect to r). The time to extinction is large when the magnitude of both r and R are small, in which case the birth rate is very small, d is approximately the magnitude of r, and the time to extinction is approximately $1/d$ (see below). In figure A1, the maximum r plotted is -0.01, and so the maximum time to extinction approaches 100 when the magnitude of r and R are small (both 0.01 at the maximum extinction time).

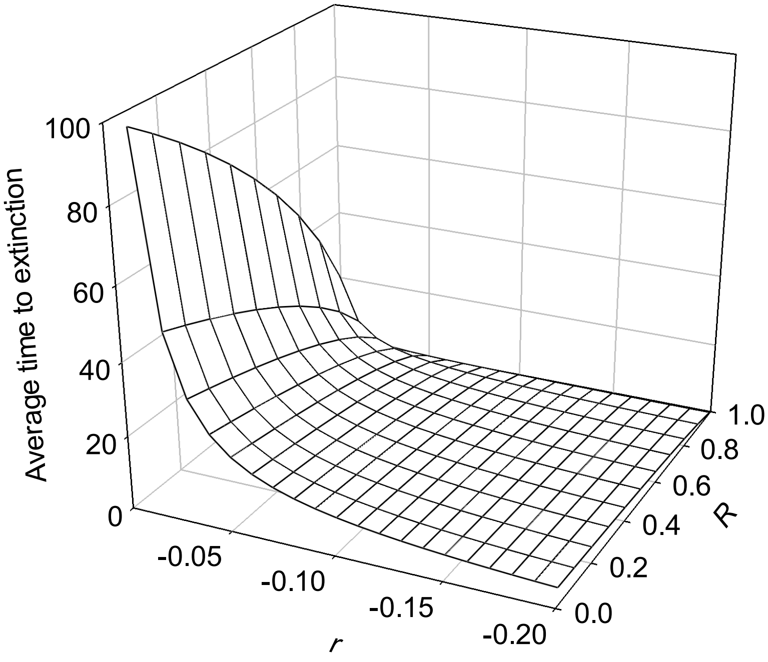

Figure A1. The mean time to extinction as a function of r and R.

If $R = 1$, then

$$E[t_e] = -TP_s\big|_0^\infty + \int_0^\infty P_s dT = \left.\frac{-T}{1+bT}\right|_0^\infty + \int_0^\infty \frac{1}{1+bT}dT = \left.\frac{-T}{1+bT}+\frac{1}{b}\ln(1+bT)\right|_0^\infty = \infty .$$

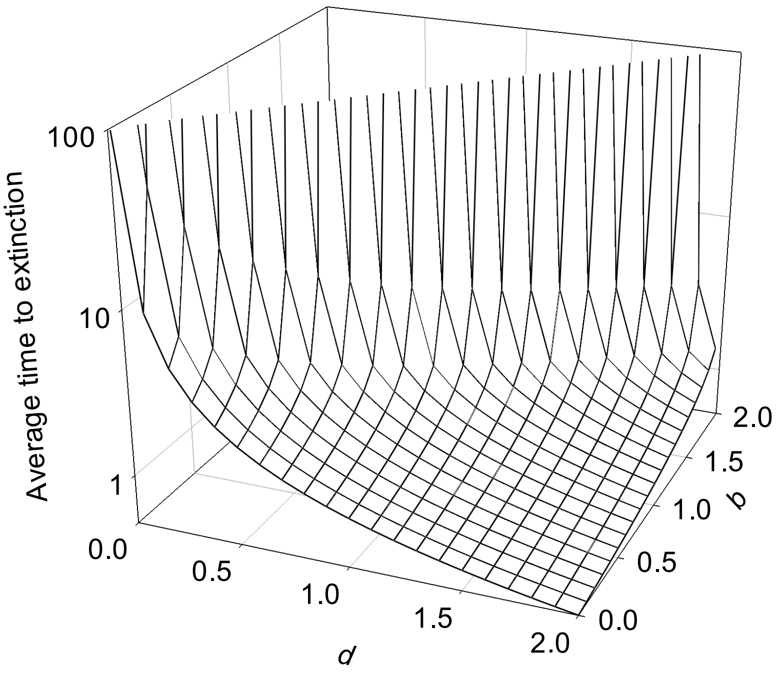

Figure A2. The mean time to extinction as a function of *b* and *d*. The mean is infinite for *b* > *d.*

The time to extinction can also be written in terms of *b* and *d* as

$$E[t_e] = \frac{(1-b/d)\ln(1-b/d)}{(b-d)b/d} = -\frac{\ln(1-b/d)}{b} = \frac{1}{d}\left[1 + \frac{b}{2d} + \frac{b^2}{3d^2} + \cdots + \frac{b^{i-1}}{id^{i-1}} + \cdots\right]$$
$$= \frac{1}{d}\left[1 + \frac{R}{2} + \frac{R^2}{3} + \cdots + \frac{R^{i-1}}{i} + \cdots\right] = \frac{1}{b}\left[R + \frac{R^2}{2} + \frac{R^3}{3} + \cdots + \frac{R^i}{i} + \cdots\right].$$

This is an increasing function of *b* and a decreasing function of *d*, and rises steeply as *b* approaches *d* (fig. A2; note the logarithmic vertical scale). The terms in brackets are sums of powers of *R* so if *R* is small, the time to extinction approaches 1/*d*, the mean time to death of the first individual (first expression on second line). For larger *R*, additional time is added as births tend to increase lineage persistence. The time to extinction is an increasing function of *R*, assuming that *d* or *b* is fixed, but from the above, it is a decreasing function of *R* if *r* is fixed. It can be shown that the derivative of the extinction time with respect to d has a greater magnitude than the derivative with respect to b, so increasing them both by the same small amount (which keeps r the same while increasing R if $b < d$) decreases the extinction time.

The average lifetime of an individual is $1/d$, so if time is measured on this scale, then

$$E[t_e / (1/d)] = \frac{d(1-R)\ln(1-R)}{rR} = \frac{d(1-b/d)\ln(1-R)}{(b-d)R} = \frac{-\ln(1-R)}{R},$$

which is an increasing function of R and not a function of r. The mean time to extinction increases with R.

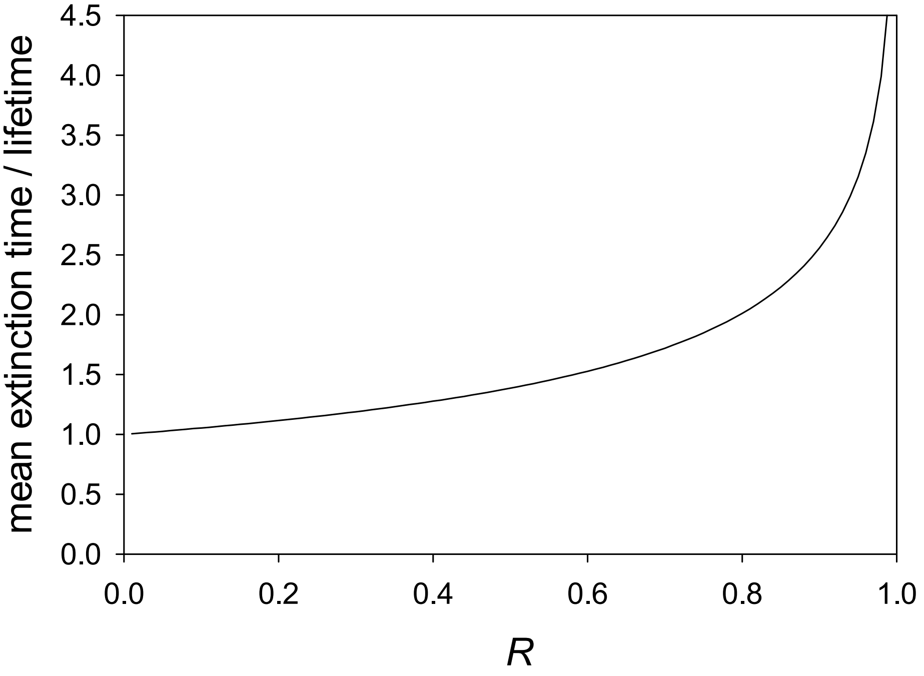

Figure A3. Mean time to extinction, divided by average lifetime, as a function of R (it is independent of r).

Median time to extinction

The median time to extinction can be found by setting the survival function to 0.5.

$$P_s = \frac{1-R}{\exp\{-rT\}-R} = 0.5,$$

and solving for T, which is $T_m = -\ln(2-R)/r$. This is defined as long as $R < 2$ (except if $R = 1$), which gives a probability of lineage persistence of less than 0.5. Again, if $r < 0$ ($R < 1$), this is a decreasing function of R and the magnitude of r (fig. A4). However, if $r > 0$ ($R > 1$), this is an increasing function of R and a decreasing function of r (fig. A5). If $R = 1$, then the median is where $P_s = 1/(1+bT) = 0.5$, which is at $T_m = 1/b$. [In terms of individual lifetime, $T_m/(1/d) = -\ln(2-R)d/r$ $= -\ln(2-R)/(b/d-1) = \ln(2-R)/(1-R)$, which is an increasing function of R and independent of r.]

At first glance, figures A1 and A5 are puzzling. For a given R, an increase in r from more to less negative values boosts persistence. This is intuitive. However, for a given r, an increase in R decreases these metrics of persistence. That is not intuitive. However, consideration of figure 5 in the main text helps clarify what is going on. Note that below the line of $b = d$ through the origin, along lines of constant r, increasing R goes along with higher values of d, and b. (The reverse is true along line of constant r that are greater than zero, i.e., the upper portion of the phase plane.) The increase in deaths looms large in determining extinction. There is no seeming paradox, if one looks at births and deaths and how they influence persistence (fig. A2); persistence is always facilitated, if births are higher, or deaths, lower. This exercise does demonstrate that usual metrics of fitness need not map neatly on the probability of persistence, even in constant environments without population structure or density dependence.

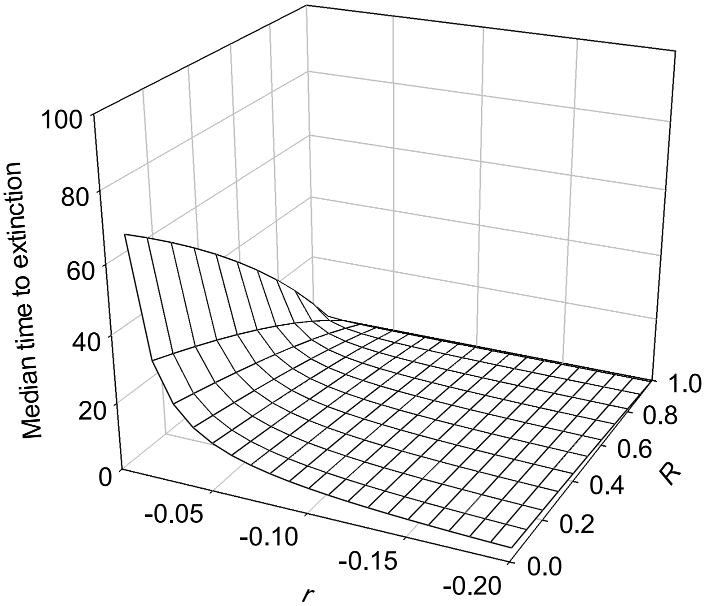

Figure A4. Median time to extinction for a population that cannot persist ($r < 0$, $R < 1$)

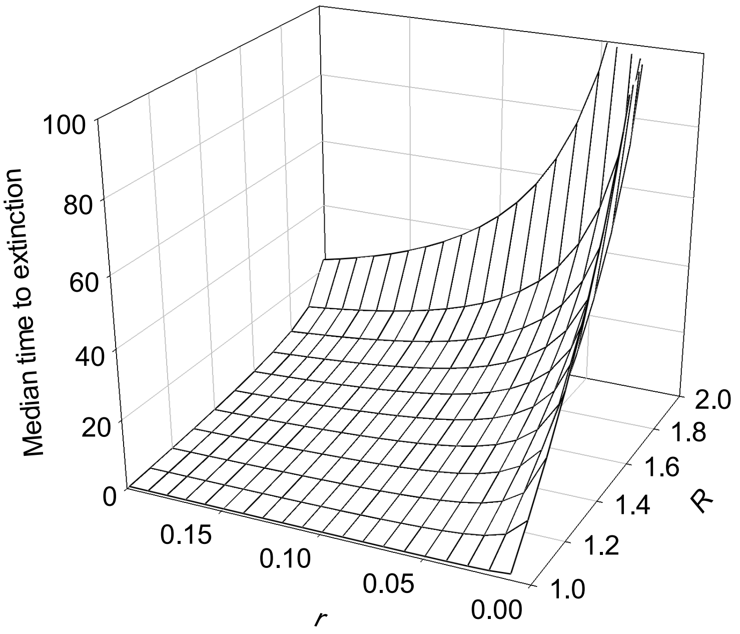

Figure A5. Median time to extinction for a population that can persist ($r > 0$, $1 < R < 2$; the last condition is needed so that the persistence probability is less than 0.5, otherwise the median extinction time is infinite).

References cited in Online Appendix

Haccou, P., P. Jagers, and V.A. Vatutin. 2005. Branching Processes: Variation, Growth, and Extinction of Populations. Cambridge University Press, Cambridge, UK.

Renshaw, E. 2013. Stochastic Population Processes. Oxford University Press.