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Reflections on niches and numbers

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Environmental factors control spatial distributions and local abundances in distinct – but overlapping – ways. Osorio-Olivera et al. examine when environments near the geometric center of a species' ecological niche – which they assume to be optimal for growth when rare – also harbor the greatest number of individuals on average at equilibrium, and when not. Transient dynamics, Allee effects and metapopulation dynamics can cloud this relationship. In this brief piece I sketch a number of further ways in which this relationship can break down, including asymmetry in the shape of the niche, spatial variation in density dependence, and nonlinear feedbacks with the environment.

Keywords: distributional ecology, Hutchinsonian niche, niche centrality hypothesis



Ecology is ‘The scientific study of the interactions that determine the distribution and abundance of organisms’ (Krebs 1994). Naturalists constantly use information about spatial patterns in abundance. A birder seeking the scarce ocellated antbird *Phaenostictus mcleannani* does not head for random points within its range, but rather aims for unbroken tracts of lowland rainforest with just the right kind of undergrowth and army ant swarms where this species is most abundant. Understanding what governs species' ranges and spatial abundance patterns is an important objective of basic ecology and also central to many applied issues, ranging from projecting the ultimate distribution and impacts of invasive species to determining where to focus conservation efforts for endangered species.

But what do the two halves of this goal – understanding distribution, and abundance – have to do with each other? A species' distribution reflects in part its ability to increase when rare – in other words, whether environmental conditions lie within its Hutchinsonian niche (sensu Hutchinson 1978, Holt 2009). Formally, the niche emerges from a function $r(e)$ – the niche response surface (Hutchinson 1978) describing dependence of population intrinsic growth rates r (= per capita birth rates minus death rates at low abundances) on the environment, e , including abiotic and biotic factors. To see the relationship between this basic concept from population ecology, and species' ranges, we can carry out a thought experiment. Divide a geographical region (e.g. a continent) into spatial units ('locations'), which vary in their environmental conditions. We introduce a moderate number of individuals of our focal species into each location, and assume there is no further dispersal among locations. The potential geographical range of a species encompasses those locations where local environmental



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conditions allow $r(e) > 0$, permitting introduced propagules to persist (Holt et al. 2005, Peterson et al. 2011); the niche is that set of environments where this inequality holds. However, persistent populations cannot increase indefinitely; direct and indirect density-dependent feedbacks (e.g. resource depletion), constrain long-term average or equilibrium abundance to some N^* (the asterisk denotes equilibrium) often measured as density (numbers per unit area) that also varies across environments – an abundance profile surface $N^*(e)$.

How are $r(e)$ and $N^*(e)$ related? Are abundances higher for environments nearer the core of the niche, with high $r(e)$ – the niche centrality hypothesis? This question, addressed by the insightful paper by Osorio-Olvera et al. (2019), has been contentious – some studies say yes (Martinez-Meyer et al. 2013), others, no (Dallas and Hastings 2018). The results of Osorio-Olvera et al. (2019) clarify potential causes for such disagreements.

I sketch their approach and then outline additional possible reasons for such discordant findings. They assume a familiar workhorse in population ecology – logistic growth – for a species occupying a heterogeneous landscape. Each cell or location (indexed by i , denoting patches, or pixels in continuous space) has a population of size N_i , whose growth depends on the local environment (e_i) as follows (ignoring complications such as Allee effects):

$$\frac{dN_i}{dt} = (r_i(e_i) - \alpha N_i) N_i + (\text{immigration into } i) - (\text{emigration from } i) \quad (1)$$

Instantaneous growth is depressed below the intrinsic growth rate by density dependence (scaled by α , assumed spatially invariant) and modified by spatial fluxes.

Given some dispersal in a temporally constant environment, species should eventually occupy locations with environmental conditions permitting a positive intrinsic growth rate – i.e. sites with conditions within the Hutchinsonian niche – (Holt et al. 2005), and grow to equilibrium, $N_i^*(e_i) = r_i(e_i) / \alpha$. Environments permitting fast growth also sustain high abundances (Williamson 1972, Holt et al. 2005).

The standard representation of logistic growth

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right)$$

obscures this potential relationship, as it seemingly implies that how fast a population grows when rare (r) is not related to its equilibrium abundance (K , the ‘carrying capacity’ known to so many students of ecology). This assumption rarely holds (Williamson 1972, Holt et al. 1997, Mallett 2012); in mechanistic models, parameters influencing density-independent growth rates typically also enter into expressions for equilibrium abundance, implying covariation. There are reasonable scenarios where r and K are biologically independent, but

this is an implausible assumption for general analyses relating niches to abundances. Osorio-Olvera et al. (2019) use the more reasonable parameterization in Eq. 1, thus permitting growth rates and equilibrium abundances to be related.

The conclusion that local abundance tracks position in niche space rests on multiple assumptions, and Osorio-Olvera et al. (2019) relax some of these to elucidate factors that can cloud the abundance–niche centrality relationship. They assume ellipsoidal niche shapes, couple local populations by dispersal, and examine what happens when distributions are not at equilibrium. Transient spatiotemporal dynamics (e.g. during early phases of an invasion) might reveal no relationship between abundance and niche centrality. Emigration bleeds numbers at high-quality sites, and immigration boosts numbers at low-quality sites, with pronounced effects given marked variability in quality among sites. Incorporating Allee effects (positive density dependence at low abundances) magnifies the obscuring effect of these spatial processes. If numbers are low for historical reasons (e.g. an isolated patch suffered a major storm), they may stay low or decline to extinction – whereas if sufficiently abundant, the population can grow. The recognition that transient dynamics and metapopulation processes (particularly given Allee effects) provide plausible reasons for not finding a signal relating ‘centrality in niche space’ and abundance is a valuable insight from the paper.

Going beyond the results of Osorio-Olvera et al. (2019), I now point out additional reasons this relationship might not hold. These include:

Asymmetric niche shapes

The geometric niche center may not be where intrinsic growth is maximal. For instance, thermal performance curves for ectotherms are asymmetric: strongly exponential at lower temperatures, peaking at high temperatures, then plummeting rapidly (Angilletta 2009, Amarasekare and Savage 2012). Similar complexities may arise in multidimensional niche space.

Spatial variation in density dependence

Osorio-Olvera et al. (2019) assume uniform density dependence across space, yet density dependence surely varies across environments. In Eq. 1, substitute $\alpha_i(e_i)$ for α , leading to equilibrium abundances, $N_i^* = r_i(e_i) / \alpha_i(e_i)$. Three possibilities arise: 1) r_i and α_i negatively covary. A species well-adapted to certain environmental conditions (as assessed by r) might also better tolerate increased density there – strengthening the correlation between niche centrality and abundance. 2) They vary independently, weakening any relationship between r and abundance within the occupied range. 3) They positively covary. Density-dependence could be stronger, and hence equilibrium abundances possibly lower, where intrinsic growth rates are higher. (If α is proportional

to r , the correlation coefficient is 1, the highest possible, but N^* is constant. To get lower N^* where r is highest requires α to be steeper than r near the peak of r .)

To illustrate this, at first glance counterintuitive possibility, consider a classical predator–prey model (Eq. 2), where a predator consumes a prey that on its own exhibits logistic growth:

$$\begin{aligned} \frac{dP}{dt} &= P[abR - C] \\ \frac{dR}{dt} &= R[r - \alpha R - aP] \end{aligned} \quad (2)$$

Here P and R respectively are predator and prey densities, a , attack rate, b converts consumption into predator births, and C is predator mortality. If prey equilibrate quickly, relative to changes in predator numbers, we set $dR/dt=0$, solve for R ,

$$R = \frac{r}{\alpha} - \frac{aP}{\alpha}$$

and substitute into the predator equation, giving:

$$\frac{dP}{dt} = P \left[\left(\frac{abr}{\alpha} - C \right) - \frac{a^2b}{\alpha} P \right] = P[r_p - \alpha_p P] \quad (3)$$

The intrinsic growth rate of the predator is $r_p \equiv \frac{abr}{\alpha} - C$, and its strength of density dependence is $\alpha_p = \frac{a^2b}{\alpha}$. Voilà, a logistic growth equation for the predator, with equilibrium abundance $P^* = r_p / \alpha_p$!

We have now expressed the intrinsic growth rate and equilibrium abundance of the predator, in terms of prey properties (its own intrinsic growth rate and density dependence), trophic parameters and predator mortality.

In principle, any of these parameters could vary as a function of environmental conditions, e , as in Eq. 1. If mortality C varies, locations with low intrinsic growth rates also have low predator abundances. But what if the attack rate varies? An ectothermic predator might forage more effectively when warmer, leading to spatial variation in attacks across thermally heterogeneous landscapes. Figure 1 shows that at relatively high attack rates, r_p and P^* are inversely related. The reason is simple – effective predators grow fast when rare, but overexploit their prey, leading in the longer run to fewer predators sustained on that prey. More broadly, careful consideration of interspecific interactions and food web feedbacks would likely reveal other reasons to doubt the generality of the niche centrality hypothesis.

Mechanistic drivers of population dynamics

Osorio-Olvera et al. (2019) used the phenomenological logistic equation (Eq. 1), as did I above. Many mechanistic models of population dynamics, however, generate non-logistic growth and imply that optimal conditions for r do not maximize equilibrium abundance (Vasseur in press). With nonlinear feedbacks, increased mortality can both reduce the intrinsic growth rate of a population (which is intuitive), and increase its equilibrium or time-averaged population size (which is not). This can occur given unstable dynamics (‘abundances’ are time-averaged means), or stage structure and density-dependent maturation rates. Abrams (2008) dubbed this counterintuitive response of abundance to elevated mortality the ‘hydra effect’, after the mythological Hydra. This surprising effect has been observed in several empirical systems, and it implies that sites where conditions permit relatively low intrinsic growth rates (because of high mortality) could sustain higher average abundances, than do sites with higher intrinsic growth rates.

To return to Osorio-Olvera et al. (2019), their valuable study places the niche-abundance debate into the context of

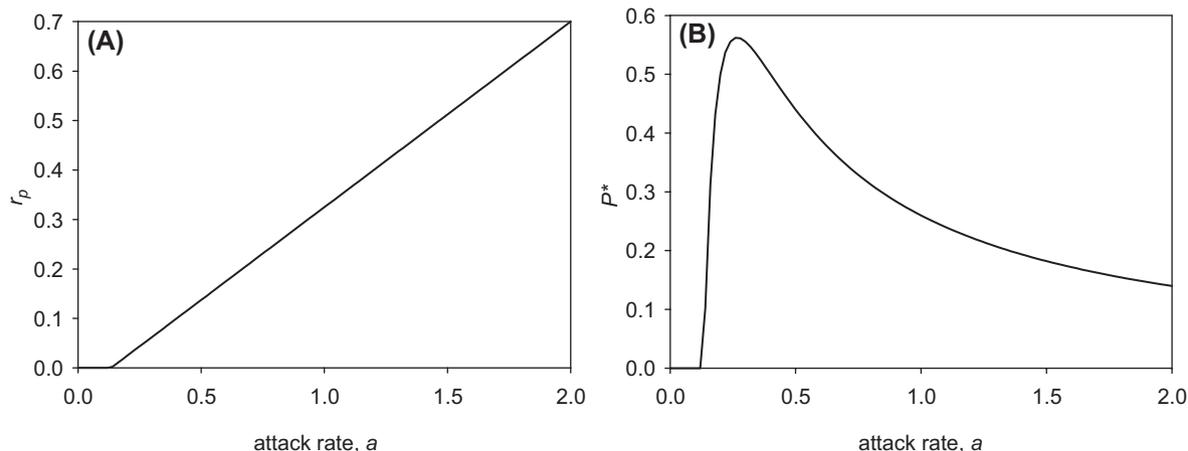


Figure 1. Predator intrinsic growth rate and equilibrium abundance as a function of attack rate for Eq. 3, showing a striking departure from the niche centrality hypothesis. In environments with high attack rates, the predator has a high intrinsic growth rate when rare, but has a low equilibrium abundance (parameters are $b=0.5$, $r=0.3$, $C=0.05$, $\alpha=0.4$).

population dynamic models, and does so in a way suggesting natural extensions. Given that humans are dramatically perturbing distributions and abundances of species across the globe, unravelling how these two basic facets of ecology are related is more important than ever.

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