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Author(s): David C. Krakauer, Karen M. Page, and Douglas H. Erwin
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Diversity, Dilemmas, and Monopolies of Niche Construction

David C. Krakauer,[1,*] Karen M. Page,[2] and Douglas H. Erwin[1,3]

1. Santa Fe Institute, Santa Fe, New Mexico 87501;
2. Department of Mathematics, University College London, Gower Street, London WC1E 6BT, United Kingdom;
3. Department of Paleobiology, MRC-121, National Museum of Natural History, Washington, DC 20013

ABSTRACT: The behavior of organisms can contribute to the transformation of their environments. When organismal impacts on the environment feed back to influence organismal density, viability, fertility, or persistence, the environment can be construed as an extension of the organism. This process of fitness-enhancing environmental transformation has been called niche construction. We focus on the relationship of niche construction with species or strain diversity and on the variability of investment in niche construction versus reproduction. We demonstrate a fundamental dilemma of niche construction, whereby the construction of a shared resource leads to a tragedy of the commons, with competition tending to eliminate niche construction strategies. The ability to monopolize a niche, either through spatial proximity or through preferential exploitation, can stabilize niche construction and promote ecological coexistence among polymorphic constructors. We consider both sympatric and allopatric origins of niche construction. Under a variety of different construction mechanisms, variability in the investment in niche construction versus reproduction suggests reproductive altruism but is fully consistent with selfish behavior. We discuss the implications of niche-construction theory on the evolution of life cycles and development, behavioral plasticity, the division of labor, and long-term macroevolutionary trends.

Keywords: niche construction, extended phenotypes, ecosystem engineering, evodevo, diversity, division of labor.

* Corresponding author; e-mail: krakauer@santafe.edu.

Niche Construction and Ecological Monopolies

A multitude of selection processes impinge on organisms, modifying their replication rates, death rates, and population densities. Through evolutionary time, species have increased their control over environmental feedback to increase or stabilize their abundance. The acquisition of such adaptations may also increase the diversity of these clades through time. There are, broadly speaking, two strategies available to achieve increased environmental control. One is to reduce the dependence of organisms on environmental factors by increasing the number of traits that insulate them from uncertainties in the environment. A second strategy is to exercise greater control over the environment by evolving features that influence environmental factors (Odling-Smee et al. 2003). In the latter case, organisms invest in traits that are associated with the construction of a niche that behaves somewhat like an extended phenotype (Dawkins 1978). The evolutionary "decision" between investing in a highly monopolistic niche (e.g., the phenotype) or the free market of niche construction ultimately depends on the source and magnitude of variation for each and the degree of control that can be exerted over (in the case of niche construction) increasingly distant spatial and temporal processes. We also distinguish niche construction, wherein feedback influences the selective regime of the species itself (Odling-Smee et al. 2003), from ecosystem engineering, wherein adaptations, behaviors, and by-products of species activities can influence the fitness of multiple species without implying a benefit to the constructor (Jones et al. 1997; Wright 2006).

A Functional and Mechanistic Classification of Niches

The niche concept endeavors to capture a large set of environmental factors relevant to the survival and reproduction of a population of organisms (Schoener 1989; Chase and Leibold 2002). The niche concept is largely associated with the work of Grinnell (1917), Elton ([1927] 2001), and Hutchinson (1959) in the first half of the twentieth century. Grinnell intended to capture the "recess" in the environment exploited by an organism while foraging. He understood that this recess is a compound of many

features, all of which are properties of the environment, that he sought to aggregate in the idea of the niche. Elton placed slightly more emphasis on the organism in its recess and the relationships of feeding among species. In other words, the Eltonian niche extends the Grinnellian niche to include some relational features between the organism and the environment. Hutchinson gave the concept a quantitative spin by defining the niche as an "*n*-dimensional hypervolume." For Hutchinson, the distinction between organism and environment was somewhat misplaced, and he proposed that ecologists would be better served by providing a specification of the organism in its environment through the niche vector. In our approach, we have cleaved to the Hutchinsonian definition by making the niche a property not only on which the organism is dependent, but also to which the organism contributes. Rather than enumerate instances of niches (see Odling-Smee et al. 2003 for a review), we classify them according to the effects that they have on different measures of organismal productivity. For example, bird nests, ant nests, and termite mounds all allow for an increase in the number of offspring and reduce extrinsic sources of mortality by providing shelter. Spiderwebs, in contrast, are primarily devices for increasing resource harvesting.

We introduce three coarse-grained, functional classes of niche construction: emphasizing the functions of a niche that serve to increase the maximum environmental carrying capacity of species, the functions that increase the effective fecundity of a species, and the functions that reduce the average mortality rate. We express these functional properties in mathematical models through their effect on variables that designate species density and niche size or range. All models consider polymorphism within two competitor species and a single, collectively constructed niche. We invoke basic life-history trade-offs by assuming that energy and time invested in niche construction is time subtracted from investment in growth and replication. Species differ in how they manage this trade-off and in the benefits they derive from the niche. This allows us to isolate costs and benefits that exclusively accrue through niche construction. In order to identify these costs and benefits, we make an operational distinction between organismal development and niche construction. Development is a niche over which a genome has a monopoly; consequently, genomes of one individual have no access to other "organismal phenotypes." The ecological niche is a free market, with no one genome possessing exclusive access but with the possibility of preferential exploitation. Somatic development and niche construction therefore lie on a continuum of "autonomy" (Krakauer and Zanotto 2009), a measure that captures variation in the dependence of individual reproduction on the collec-

tive products of a population of heterogeneous genomes or behavioral strategies.

A Comment on Earlier Models

The models presented in this article differ from previous contributions to niche-construction theory (e.g., see Gurney and Lawton 1996; Laland et al. 1996; Silver and Paolo 2006) in three important ways. First, and most important, the niche is treated as an additional dynamical system to that describing organismal evolution and behavior. Hence, the niche is not represented indirectly through an algebraic viability function but directly through a differential equation. Second, unlike previous models, we do not attempt to model the genetics and Mendelian inheritance of niche construction but rather the phenotypic or ecological level of transformation. Third, we explore a diverse set of construction mechanisms rather than a generalized frequency-dependent effect. These models differ from those of Odling-Smee and colleagues (Laland et al. 1996) by moving the emphasis from population genetics and transmission toward population dynamics and mechanisms of niche control. We consider both approaches to be important, because each reveals complementary aspects of the niche-construction process.

In the following theory subsections, we present several functional niche-construction models and their stationary or long-term distributional properties. These subsections will be fairly mathematical with respect to the quantity of algebra and will present the principal results. For those wishing to avoid the detailed analysis, the key results from each model are summarized qualitatively, and then in greater detail, in the subsections that follow. In these subsections, the models are placed in the context of prior research and relevant empirical studies.

Carrying Capacity Construction

First we consider the case in which niche construction serves to increase the effective environmental carrying capacity. The carrying capacity is determined through a mixture of organismal behavior and physiology and environmental resource limitations. Organisms from two species have a choice of investing in increased rates of replication and growth or investing in the construction of a niche that increases the maximum population density for both species. This raises questions about the relationship of altruism to niche construction, because niche construction makes essential resources available to others at a cost of reduced reproduction to oneself. Throughout, species are assumed to be in competition over resources. Table 1 provides definitions of parameters and variables used in this article. We consider a model of two species (*x* and *y*)

Table 1: Parameter and variable definitions employed in niche-construction models

Parameter	Definition
x, y	Density of competing species
r_i	Birth rate parameter of species i
λ_i	Death rate parameter of species i
z	Constructed niche
c_i	Niche-construction parameter of species i (no construction when $c_i = 1$)
w	Density of mutant strain differing in level of niche construction
c'	Level of niche construction by mutant strain w
p	Background rate of niche construction (abiotic processes and ecosystem engineering)
d	Rate constant of niche degradation (modulates niche inheritance)
b_{ij}	Competitive impact of species i on species j
e	Efficiency of niche construction
k_i	Efficiency of resource extraction from the niche by strain or species i
k	Efficiency of resource extraction when $k_i = k$ for $\forall i$
m	Monopolization parameter determining quantity of niche than can be controlled
z_i(effective)	The niche available to a species or strain once monopolized
L_i	Niche use efficiency in reducing death rate of species i

contributing to a single niche (z), where the niche decays at a rate (dz) that is typically slower than that of organismal death rates (for an extension to multiple species, see app. B in the online edition of the *American Naturalist*). The niche can also be constructed slowly through processes, independent of the two focal species, that we think of as a combination of abiotic processes and ecosystem engineering (Jones et al. 1994; Wright 2006) by third-party species in the ecosystem. We express the dynamics of competitive niche construction through a system of differential equations:

$$\dot{x} = c_x x - x \frac{x + b_{yx} y}{k_x z}, \tag{1}$$

$$\dot{y} = c_y y - y \frac{y + b_{xy} x}{k_y z}, \tag{2}$$

$$\dot{z} = p + (1 - c_x) \frac{ex}{x + y + z}$$

$$+ (1 - c_y) \frac{ey}{x + y + z} - dz. \tag{3}$$

In these equations, the parameters c_i are bounded between 0 and 1 and capture the differential investment in

reproduction versus niche construction. A lineage i does not engage in niche construction when $c_i = 1$. The parameters k_i are organismal features that describe the ability of organisms to extract resources from the constructed niche. The parameters b_{ij} are the competition coefficients. Energy expended directly on replication and energy expended on niche construction are not equally efficient. In contrast to the more isolated processes of development and replication constituting ontogeny, there are many processes outside of the control of the organism influencing niche construction. We capture the increased efficiency of reproduction and development through a parameter e. A value of $e < 1$ measures a quantity of biomass that could have been invested in growth that becomes dissipated during niche construction. The organism-independent rate of construction is given by p. If we consider only the ecological dynamics, ignoring in this subsection the evolutionary dynamics of niche construction, we can derive the equilibrium solutions for this model: (1) $x = y = 0$ (which is always unstable); (2) $x = 0$, $y = k_y c_y z$, and $z = p/d + \{[(1 - c_y)ek_y c_y]/[d(k_y c_y + 1)]\}$ (which is stable if and only if $k_x c_x < b_{yx} k_y c_y$); (3) $y = 0$, $x = k_x c_x z$, and $z = p/d + \{[(1 - c_x)ek_x c_x]/[d(k_x c_x + 1)]\}$ (which is stable if and only if $k_y c_y < b_{xy} k_x c_x$); and (4) the coexistence state $x = z[(k_x c_x - b_{yx} k_y c_y)/(1 - b_{yx} bxy)]$ and $y = z[(k_y c_y - b_{xy} k_x c_x)/(1 - b_{yx} bxy)]$.

In the single-species solutions, the density of each species increases with natural processes of construction p and an increase in the efficiency of niche exploitation and is maximum for an intermediate value of niche construction c_y. Longer-lived niches also increase density. In the coexistence regimes, competition tends to reduce population densities.

The Construction Dilemma

The previous ecological analysis conceals a fundamental instability property of niche construction and a possible source of its exclusion over the course of evolutionary time. Niche construction acquires an altruistic character when the niche cannot be perfectly monopolized by an individual. Shared access to common parts of a niche would seem to imply that it pays off to invest in reproduction at the expense of niche construction. We can formally demonstrate this by considering the invasion dynamics of a mutant that differs only in its level of niche construction.

The single-species steady state population density in the model above varies with c_x. The maximal density will occur for an intermediate value of c_x (in this case, for some value of c_x in the interval [1/2, 2/3]). The problem is that evolution need not lead to maximal population density because there is competition over a shared resource that is

costly to produce. This leads to a tragedy of the commons. Consider a single-species population. Assume a wild-type population of density x with construction parameter c. Suppose we introduce a rare mutant strain with parameter c'. The mutant has density w, initially a small value, and the other parameters are the same: $k_w = k_x = k$ and $b_{wx} = b_{xw} = 1$. The equations become

$$\dot{x} = cx - x\frac{x + w}{kz}, \tag{4}$$

$$\dot{w} = c'w - w\frac{w + x}{kz}, \tag{5}$$

$$\dot{z} = p + (1 - c)\frac{ex}{x + w + z}$$

$$+ (1 - c')\frac{ew}{x + w + z} - dz. \tag{6}$$

Thus,

$$\frac{\dot{w}}{w} = \frac{\dot{x}}{x} + (c' - c), \tag{7}$$

and so

$$\frac{w}{w(0)} = \frac{x}{x(0)} e^{(c'-c)t}. \tag{8}$$

Because w and x are bounded from above, if $c' > c$, then $x \to 0$, and if $c' < c$, then $w \to 0$. If c is free to evolve, it will increase to 1.

Strain competition in this simplified version of the model leads to investment in reproduction at the expense of niche construction, even though this means that the population density becomes small. At a value of $c = 1$, the species is not constructing a niche and therefore the steady state value of z will be p/d, which will be small. The population will still subsist at a steady density of $x = kp/d$. The dynamics of the construction dilemma are illustrated numerically in figure 1.

Niche Monopolies Can Overcome the Construction Dilemma

We have observed that models of evolutionary dynamics preclude the possibility of niche construction evolving even within a single species when there are strains differing in the value of c. However, these models neglect important features of niche construction relating to preferential access and control of the niche. When a niche is constructed, it typically has a spatial location and is preferentially ex-

ploited by individuals in that location. Moreover, organisms might be expected to preferentially control and thereby exploit niches that they themselves have constructed. In this way, they might defend their own niches and effectively monopolize them.

Consider an extended model in which an individual has a probability $m \in [0, 1]$ of monopolizing its own niche and a probability $1 - m$ of exploiting another's niche. Consider a population of wild-type individuals of density x and a population of a rare mutant strain of density w. The niche constructed by wild-type individuals has density z_x and that constructed by the mutant has density z_w. Let us assume that $p = 0$ in the model, so that the niche arises only through construction.

The niche available to the wild-type individuals has magnitude

$$z_x(\text{effective}) \approx z_x m + z_x(1 - m) = z_x,$$

and that available to a rare mutant has magnitude

$$z_w(\text{effective}) \approx z_w m + z_x(1 - m),$$

where z_w is the amount of niche constructed by the mutant individual. If we now assume that the per-individual amount of niche constructed is roughly proportional to $1 - c$ (see app. C in the online edition of the *American Naturalist*), then

$$z_w \approx z_x \frac{1 - c'}{1 - c}.$$

The per capita growth rate of the rare mutant is

$$\approx c' - \frac{x_*}{kz_w(\text{effective})}$$

$$= c' - c\frac{z_x}{z_x(1 - m) + z_x m(1 - c')/(1 - c)},$$

where x_* is the steady state value of x in the absence of the mutant. The rare mutant can grow if and only if $c'[(1 - m)(1 - c) + m(1 - c')] > c(1 - c)$. If mutants have $c' - c \ll 1$, then the mutants that can invade have $c' > c$ if and only if $c < 1/(1 + m)$. Thus, if we introduce rare mutant strains with a construction parameter close to the wild-type value, then evolution will tend toward a value of this parameter equal to

$$c = \frac{1}{1 + m}. \tag{9}$$

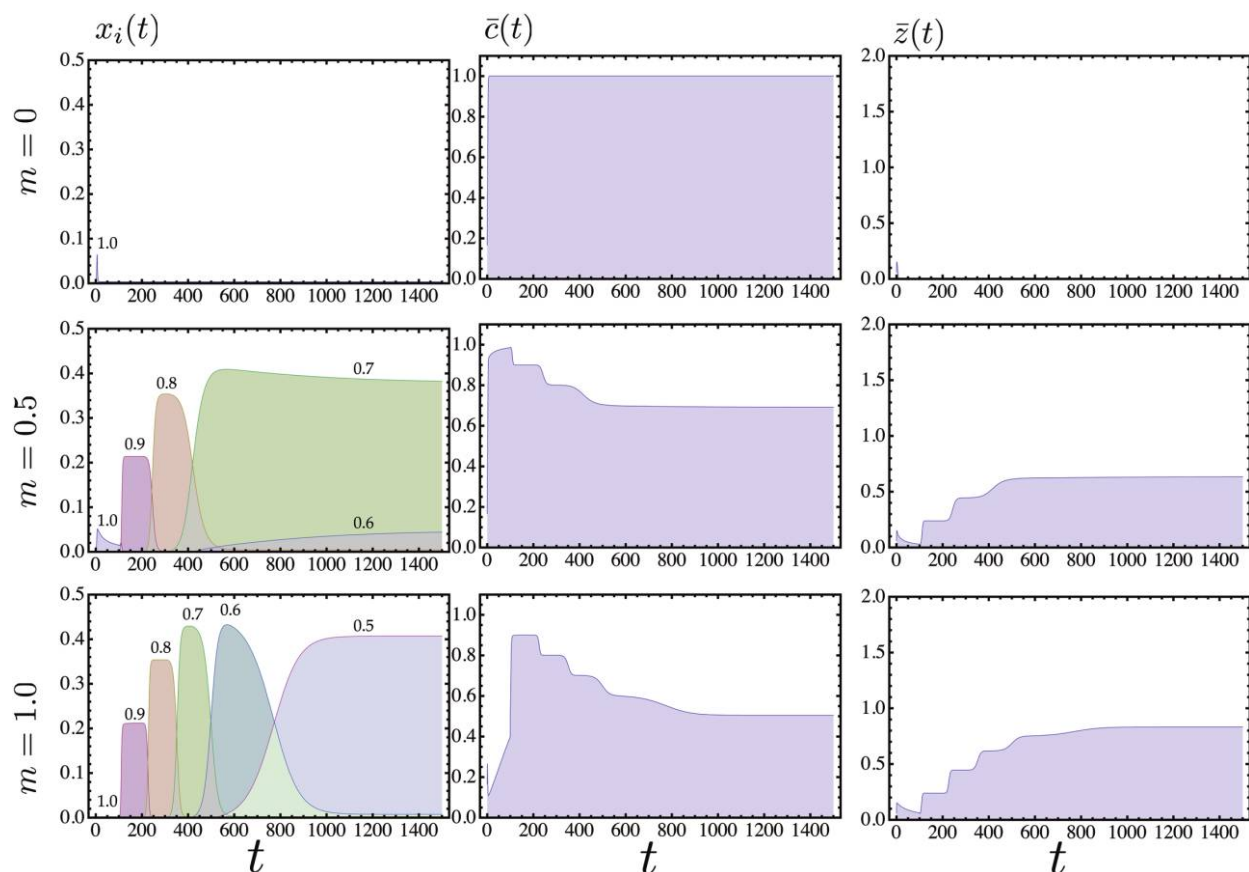Recall that m is the probability that an individual is able

Figure 1: Monopolies and the niche-construction dilemma (*top*). Starting with a strain x_1 with $c_{max} = 1.0$, we introduce a new strain of x_i every 100 time steps. Strains differ in the value of c_i by a real interval of 10^{-1}, reaching a minimum strain value of $c_{min} = 0.5$, which invests equally in reproduction and niche construction, at $t = 600$. Here, $m = 0$, and hence there is no ability to monopolize the shared niche. Strains with smaller values of c_i, corresponding to higher rates of niche construction, are unable to invade; hence, the population average investment in niche construction $(1 - \bar{c}(t) = 0)$ is negligible, the density of the dominant strain remains constant, and the average level of niche construction $(\bar{z}(t))$ remains very low (*middle*). We now allow for partial monopolies ($m = 0.5$), and we observe that niche-constructing strains can invade the population, thereby systematically increasing the per capita level of niche construction and increasing the total niche abundance. For intermediate monopolies we also observe coexistence of different degrees of niche construction (*bottom*). When there are perfect monopolies ($m = 1.0$), the level of niche construction evolves to its maximum under carrying capacity construction at $1/(1 + m)$, excluding all alternative strategies. The parameter set is $e = 10$, $k_x = k_w = 10$, $kb_{xw} = b_{wx} = 1$, $p = 0.001$, $d = 2$, and the total number of mutant, niche-constructing strains is $S = 6$.

to control and thereby exploit its own niche rather than the niche constructed by a competitor. If there is no ability to monopolize a niche ($m \approx 0$), then, as per the dilemma, c tends toward 1. If an individual is able to ensure exclusive access to its own niche ($m = 1$), then evolution leads to $c = 1/2$.

The ability to alter the probability that an individual exploits its own niche m causes the ecological dynamics described above to be somewhat altered. The single-species steady states remain the same, but the population densities at the coexistence state now depend on m. The stability conditions for the single-species state with x only becomes

$$b_{xy}c_x k_x > c_y k_y \left[(1 - m) + m \frac{1 - c_y}{1 - c_x} \right]. \tag{10}$$

The inclusion of the possibility of monopolies adds a term to the stability condition that captures the relative advantage of niche construction to species x.

Ecology after Evolution: Allopatric Evolution of Niche Construction

If two species evolve in isolation from each other, their c values should both tend toward $1/(m + 1)$, as per previous

results. We now ask, if the two populations become mixed, what influence do these allopatrically evolved c values have on the stability of the steady states in sympatry?

We find that, if the values of c for the two species are equal (including the case in which they both take the value $1/(m + 1)$), the x-only state is stable if and only if

$$b_{xy}k_x > k_y.$$

If $c_x = 1/(m + 1)$ and $c_y = c_x + \Delta c$, then the condition for stability for the x-only state is given by

$$b_{xy}k_x > k_y[1 - (1 + m)^2(\Delta c)^2],$$

where $\Delta c \ll 1$. So, for $\Delta c \neq 0$ (whether positive or negative), the condition for stability of the x-only state is weaker than when both c values are identical. For all other values of c_x, there are values of Δc that make the stability condition stronger. Thus, although the stability condition for the x-only state depends on the parameters b_{xy}, k_x, and k_y, for fixed values of these parameters, x has the best chance of outcompeting y (strictly, the x-only state has the greatest chance of stability) if $c_x = 1/(m + 1)$, the value toward which it evolved when allopatric. In addition, y has the best chance of invading x (strictly, the x-only state has the smallest chance of stability) if $c_y = 1/(m + 1)$.

Competitive Niche Construction: Sympatric Evolution of Niche Construction

We now consider the previous model and suppose that two species of density x and y exist in sympatry at steady state. A rare mutant, with a different c value, is introduced. It has abundance w, which is initially small. We seek to determine whether it can invade. The remaining parameters relating to strain w are the same as for x, and we drop the suffixes on these parameters. The equations become

$$\dot{x} = cx - x\frac{x + b_{yx}y}{k_x z_x(\text{effective})},\tag{11}$$

$$\dot{y} = c_y y - y\frac{y + b_{xy}x}{k_y z_y(\text{effective})},\tag{12}$$

$$\dot{w} = c'w - w\frac{x + b_{yx}y}{k_x z_w(\text{effective})},\tag{13}$$

where $z_i(\text{effective}) = mz_i[(x + y + w)/i] + (1 - m)z$ for $i = x, y, w$ and $z = z_x + z_w + z_y$ (see app. C for details), where we assume that w and z_w are negligibly small. In fact, when w is rare, $z \approx z_x + z_y$ because there is a negligible niche constructed by the rare mutant. The mutant z_w

should be counted only in the monopolizable niche of a few mutant individuals, since the amount of niche per individual is nonnegligible. In the expression for $z_w(\text{effective})$, we assume that, for small values of p, $z_w/[(1 - c')w] \approx z_x/[(1 - c)x]$ (see app. C). The per capita growth rate of w is positive if and only if

$$c'z_w(\text{effective}) > cz_x(\text{effective}).\tag{14}$$

Now,

$$z_x(\text{effective}) \approx (1 - m)(z_x + z_y) + m\frac{y + x}{x}z_x,$$

$$z_w(\text{effective}) \approx (1 - m)(z_x + z_y) + m\frac{1 - c'}{1 - c}\frac{y + x}{x}z_x.$$

Therefore, w can invade if and only if

$$c < c_{\text{crit}} \equiv \frac{1 + (z_y/z_x)(1 - m) + m(y/x)}{1 + m + (1 - m)(z_y/z_x) + m(y/x)}.\tag{15}$$

Thus, evolution leads c to an intermediate value of c_{crit}. If the niche is at least partly monopolizable, then carrying capacity construction occurs even in the sympatric presence of a competitor species.

Fecundity Construction

Not all niche construction is expected to result in an increase in the environmental carrying capacity. In many cases, the niche serves to increase the fecundity of a species. Consider nests of various kinds that serve to modulate fertility and mortality rates. In this section, we develop models to capture niche-construction activity that increases fecundity. As before, we first consider a two-species system and a single niche, considering the ecological dynamics and not the evolutionary dynamics. In this case, the niche contributes directly to the rate of growth:

$$\dot{x} = c_x r_x x\frac{z}{z + k_x(x + b_{yx}y)} - \lambda_x x,\tag{16}$$

$$\dot{y} = c_y r_y y\frac{z}{z + k_y(b_{xy}x + y)} - \lambda_y y,\tag{17}$$

$$\dot{z} = p + (1 - c_x)\frac{ex}{x + y + z}$$

$$+ (1 - c_y)\frac{ey}{x + y + z} - dz.\tag{18}$$

This model explicitly includes the birth rates r_x and r_y and the death rates λ_x and λ_y for each species. The steady states

of this model have either $x = 0$, $y = 0$; $x = 0$, $y \neq 0$; $x \neq 0$, $y = 0$; or coexistence. For the single-species, competitive equilibrium we find

$$y = 0,$$

$$x = \frac{c_x r_x - \lambda_x}{\lambda_x k_x} z \equiv U_x z,$$

$$z = \frac{p}{d} + \frac{e}{d} \frac{U_x(1 - c_x)}{U_x + 1}.$$

The resource use efficiency of species x is given by U_x and the steady state value has $x = U_x(p/d) + (e/d)\{[U_x^2(1 - c_x)]/(U_x + 1)\}$, where $(e/d)\{[U_x(1 - c_x)]/(U_x + 1)\}$ is the maximal amount of z that is constructable by species x. For stability of this state, we require that

$$b_{xy}U_x \equiv b_{xy}\frac{c_x r_x - \lambda_x}{\lambda_x k_x} > \frac{c_y r_y - \lambda_y}{\lambda_y k_y} \equiv U_y. \quad (19)$$

For $b_{xy} > U_y/U_x$ and $b_{yx} > U_x/U_y$, both single-species competitive equilibria are stable. This indicates that, when the competition coefficients are larger than the ratios of resource use, either species is capable of outcompeting the other if initially suitably abundant.

This model has a coexistence steady state in addition to the zero state and single-species states, with $y = 0$, $x \neq 0$ and $x = 0$, $y \neq 0$. This state is given by

$$x = \frac{1}{1 - b_{xy}b_{yx}}(U_x - b_{yx}U_y)z \equiv A_x z,$$

$$y = \frac{1}{1 - b_{xy}b_{yx}}(U_y - b_{xy}U_x)z \equiv A_y z,$$

where z is given by

$$z = \frac{p}{d} + \frac{e}{d} \frac{A_x(1 - c_x) + A_y(1 - c_y)}{1 + A_x + A_y}. \quad (20)$$

If $c_x r_x - \lambda_x > 0$ or $c_y r_y - \lambda_y > 0$ (otherwise the zero state is the only steady state), then the zero state is always unstable.

The Construction Dilemma

As with carrying capacity construction, there is little reason to expect evolution to lead to any appreciable niche construction. The construction dilemma suggests that individuals would be better off by investing solely in reproduction.

We consider a wild-type population of density x with niche construction parameter c. Suppose we introduce a rare mutant strain with parameter c'. The mutant has density w, initially a small value, and the other parameters are the same: $k_w = k_x = k$, $r_w = r_x = r$, $\lambda_w = \lambda_x = \lambda$, and $b_{xw} = b_{wx} = 1$. The equations become

$$\dot{x} = crx\frac{z}{z + k(x + w)} - \lambda x, \quad (21)$$

$$\dot{w} = c'rw\frac{z}{z + k(x + w)} - \lambda w, \quad (22)$$

$$\dot{z} = p + (1 - c)\frac{ex}{x + w + z}$$

$$+ (1 - c')\frac{ew}{x + w + z} - dz. \quad (23)$$

Thus, if $c' > c$, then $x \rightarrow 0$, and if $c' < c$, then $w \rightarrow 0$. If c is allowed to evolve, it will increase to 1. With c approaching 1, there will be negligible niche constructed, and so z will take a value p/d, which we assume to be small. Consequently, the single species present will have low abundance.

Niche Monopolies Can Overcome the Construction Dilemma

As before, we now allow for probability $m \in [0, 1]$ of monopoly and probability $1 - m$ of gaining access to another's niche. Consider a population of wild-type individuals of density x and a rare mutant strain of density w. The niche constructed by wild-type individuals has density z_x, and that constructed by the mutant has density z_w.

The niche available to the wild type has a density

$$z_x(\text{effective}) \approx z_x,$$

and that available to the mutant has density

$$z_w(\text{effective}) \approx z_w m + z_x(1 - m),$$

where $z_w \approx z_x(1 - c')/(1 - c)$, assuming that $p \approx 0$ and z_w is in quasi equilibrium with w. The per capita growth rate of the rare mutant is

$$\approx c'r\frac{z_w(\text{effective})}{z_w(\text{effective}) + kx_*} - \lambda,$$

where x_* is the steady state value of x in the absence of the mutant. Now,

$$cr\frac{z_x}{z_x + kx_*} = \lambda,$$

so the growth rate is positive and the mutant invades if and only if

$$(c'r - \lambda)z_w(\text{effective}) > (cr - \lambda)z_x. \qquad (24)$$

Let $c' - c = \Delta c$, and suppose this is small. The mutant can invade if and only if

$$\Delta cr(1 - c - m\Delta c) > \Delta cm(cr - \lambda). \qquad (25)$$

Thus, mutants with $c' > c$ can invade if and only if

$$c < \frac{1 + m\lambda/r}{1 + m}. \qquad (26)$$

The condition for any species to persist is that $cr > \lambda$, which implies that $r > \lambda$. If c is allowed to evolve, it will reach an intermediate value of $(1 + m\lambda/r)/(1 + m)$. When there is no monopolizing of the niche ($m \approx 0$), then, as per the prior model with no preferential access, c tends to 1. If an individual is able to perfectly monopolize the niche ($m = 1$), then evolution leads to $c = 1/2 + \lambda/2r$. Note that the evolved value of c is greater than $1/(1 + m)$ and thus is at a lower level of niche construction than it is for carrying capacity construction.

The evolved level of niche construction decreases with an increase in the death rate and increases with an increase in the niche-independent replication rate. Longer-lived species do better by investing in niche construction that augments fecundity. Short-lived species with high fecundity benefit less from niche construction.

The ability of individuals to monopolize a niche alters the purely ecological dynamics. The single-species steady states remain the same, but the population densities at the coexistence state once again depend on m. The stability condition for the single-species state with x is approximately $b_{xy}U_x > U_y\{(1 - m) + m[(1 - c_y)/(1 - c_x)]\}$.

Ecology after Evolution: Allopatric Evolution of Niche Construction

If two species evolve in isolation from each other, their c values should tend to

$$c_x = \frac{1 + m(\lambda_x/r_x)}{1 + m},$$

$$c_y = \frac{1 + m(\lambda_y/r_y)}{1 + m}.$$

We can now ask, if the populations are then mixed, what influence do these evolved c values have on the stability of the allopatric steady states? We do not find, as per "Ecology after Evolution: Allopatric Evolution of Niche Construction" earlier, that the allopatrically evolved values are optimal in terms of ensuring the stability of each of the single-species states against invasion by another species and allowing the species to invade the other.

The stability of the x-only state to invasion by y would be maximized by a value of c_x that is the smaller root of

$$(1 - m)c_x^2 - 2c_x(1 - mc_y) + 1 + \frac{m\lambda_x}{r_x} = 0, \qquad (27)$$

whereas the stability of the x-only state to invasion by y would by minimized by

$$c_y = (1 - m)\frac{1 - c_x}{2m} + \frac{1}{2} + \frac{\lambda_y}{2r_y}, \qquad (28)$$

assuming this value is less than 1. These values of c_x and c_y are not likely to evolve under any realistic population dynamics. They merely serve to illustrate that allopatric evolution of fecundity construction does not maximize the stability of the single-species state in the face of interspecific competition, as it does under carrying capacity construction.

Competitive Niche Construction: Sympatric Evolution of Niche Construction

As in the earlier model "Competitive Niche Construction: Sympatric Evolution of Niche Construction," we suppose that two species of density x and y exist at steady state. A rare mutant, one with a different c value, is introduced. It has a value of abundance w that is initially small. We determine whether it can invade. The remaining parameters relating to strain w are the same as for x, and we drop the suffixes on these parameters. The equations become

$$\dot{x} = crx\frac{z_x(\text{effective})}{z_x(\text{effective}) + k(x + w + b_{yx}y)} - \lambda x, \qquad (29)$$

$$\dot{w} = c'rw\frac{z_w(\text{effective})}{z_w(\text{effective}) + k(x + w + b_{yx}y)} - \lambda w, \qquad (30)$$

$$\dot{y} = c_y r_y y\frac{z_y(\text{effective})}{z_y(\text{effective}) + k_y[y + b_{xy}(x + w)]} - \lambda y, \qquad (31)$$

$$\dot{z} = p + (1 - c)\frac{ex}{x + y + w + z}$$
$$+ (1 - c')\frac{ew}{x + y + w + z} \qquad (32)$$
$$+ (1 - c_y)\frac{ey}{x + y + w + z} - dz,$$

where $z_i(\text{effective}) = mz_i[(x + y + w)/i] + (1 - m)z$ for $i = x, y, w$ and $z = z_x + z_w + z_y$, as in "Competitive Niche Construction: Sympatric Evolution of Niche Construction" earlier. We assume now that $p \approx 0$.

We have

$$\dot{z}_x = (1 - c)\frac{ex}{x + y + w + z} - dz_x, \qquad (33)$$

$$\dot{z}_y = (1 - c_y)\frac{ey}{x + y + w + z} - dz_y. \qquad (34)$$

The per capita growth rate of the rare mutant is approximated by

$$\frac{\dot{w}}{w} = c'r\frac{z_w(\text{effective})}{z_w(\text{effective}) + k(x_* + b_{yx}y_*)} - \lambda, \qquad (35)$$

where x_* and y_* are the steady state values of x and y in the absence of w and $z_w(\text{effective})$ takes the value that it does when x and y are at steady state and w is small.

The per capita growth rate for a mutant with $c' > c$ is positive, and so the mutant invades if and only if

$$(c'r - \lambda)z_w(\text{effective}) > (cr - \lambda)z_x(\text{effective}), \qquad (36)$$

which is true for $c' > c$ and c' close to c if and only if

$$c < c_{\text{crit}} \equiv \frac{1 + m(\lambda/r) + (z_y/z_x)(1 - m) + m(y/x)[1 + (\lambda/r)]}{1 + m + (z_y/z_x)(1 - m) + 2m(y/x)},$$

$$(37)$$

where x, y, z_x, and z_y take their steady state values in the absence of w. Selection on niche construction leads c to a value c_{crit}. It is straightforward to see that this ensures that evolution terminates at an intermediate value of c. Thus, if the niche is at least partly monopolizable, then fecundity construction occurs even in the continuous presence of a competitor species.

Mortality-Related Construction

In addition to increasing the carrying capacity and increasing growth rates, niches can reduce the level of mortality. For example, burrowing in sediment can provide protection from predators as well as access to food. We ask how species that construct protective niches should invest in niche construction. For this question, we explore the system

$$\dot{x} = c_xr_xx - \frac{\lambda_x(x + b_{yx}y)}{(x + b_{yx}y) + L_xz}x, \qquad (38)$$

$$\dot{y} = c_yr_yy - \frac{\lambda_y(y + b_{xy}x)}{(y + b_{xy}x) + L_yz}y, \qquad (39)$$

$$\dot{z} = p + (1 - c_x)\frac{ex}{x + y + z} \qquad (40)$$

$$+ (1 - c_y)\frac{ey}{x + y + z} - dz.$$

This model can be shown to be effectively equivalent to fecundity construction, provided $\lambda_x > c_xr_x$ and $\lambda_y > c_yr_y$ in this model and $\lambda_x < c_xr_x$ and $\lambda_y < c_yr_y$ in the fecundity construction model. These inequalities correspond to the positive and bounded steady state values of x and y and so will typically apply. Because this model behaves in essentially the same way as the fecundity construction model, we do not analyze it further.

Qualitative Summary of Theory

We have considered several mechanisms and trade-offs related to the adaptive, organismal construction of environments. We have analyzed the following regularities: the relationship of niche construction on species diversity, the impact of construction on strain diversity within a species, variability in the level of niche construction within a population, patterns in the evolution of niche construction assuming either allopatric or sympatric population structure, and several life-history characteristics of a species influencing the evolution of niche construction. Throughout, we have imposed a life-history trade-off, whereby investment in niche construction subtracts from investment in reproduction.

We find that, under conditions of within-species strain competition, niche construction is typically abandoned in favor of investment in reproduction. We refer to this as the construction dilemma. We suggest that this dilemma represents a significant obstacle to niche construction in populations where strains of a single species, or multiple species, have access to a shared niche.

When we allow for active niche monopolization, construction is restored. Niche monopolization allows a niche to be partitioned into a resource over which individuals have preferential access when they themselves have constructed it. This is assumed to reflect spatial privileges, niche defense, and mechanical advantages derived from "knowledge" of niche properties. The evolutionarily stable level of niche construction increases with increasing monopolization to a maximum level of around one-half of

effort/energy put into reproduction and one-half into niche construction.

The evolutionarily stable level of niche construction is dependent on whether construction evolves in sympatric or allopatric populations. For carrying capacity construction, the two-species allopatric optimum maximizes the stability of species that become sympatric. For fecundity construction, this is not the case, and the allopatric optimum can be invaded by a competitor species not at its own constructing optimum if it is more effective at exploiting the shared resources of the niche.

Under conditions promoting species coexistence with the possibility of monopolization, high levels of niche construction and niche exploitation prevail. The efficiency of energy conversion into niches, relative to reproduction, is a crucial determinant of species diversity. When construction is relatively inefficient, species need to be poor competitors in order for the population to remain diverse and for niche construction to be stabilized. When construction is efficient, species need to be strong competitors in order to invest heavily in niche construction.

We find that, generally, under all three model classes, intermediate levels of niche construction tend to evolve, with investment spread equitably over reproduction and niche construction. For fecundity construction, the investment in construction tends to decrease with increasing death rates (short-lived species) and increase in species with high rates of reproduction. In this way, coexisting species or strains can differ greatly in the level of niche construction and reproduction while remaining competitive.

Quantitative Summary of Theory

Carrying Capacity Construction I

1. When two species are in competition, they evolve to a single-species community when the ratio of their carrying capacity coefficients multiplied by their niche-construction level is less than their coefficients of competition. Thus, species j outcompetes species i when $k_i c_i / k_j c_j < b_{ji}$. In other words, this occurs when the per capita reduction in the density of i through the behavior of j is greater than any carrying capacity advantage held by i.

2. Species i and j coexist when their relative carrying capacity is greater than the competitive reduction in density. Coexistence implies that efficient niche exploiters who do not invest much in niche construction are poor competitors.

3. The individually selected, stable level of niche construction tends toward 0, assuming that there is strain variation within a species. Thus, when there are trade-offs

between reproduction and niche construction and when niches can be exploited by different strains within a species or by different species, niche construction is neglected in favor of reproduction. This is the construction dilemma.

4. The ability to monopolize a niche restores niche construction. In particular, if we define the effective niche of x when in competition with y as z_x(effective) $\approx z_x m[(x + y)/x] + (z_x + z_y)(1 - m)$, then niche construction evolves to an intermediate, stable value given by $1/(1 + m)$. Thus, as control over a niche increases, so does the level of niche construction.

5. When the level of niche construction within a species evolves in allopatry, then the stable value $1/(1 + m)$ is optimally competitive in the face of a competitor species when mixed.

6. When the level of niche construction within a species evolves in sympatry with a second species, the niche-construction value $1/(1 + m)$ does not evolve. Competition within a species and competition between species can favor different levels of niche construction.

Fecundity and Mortality-Related Construction

1. The stability properties of the niche-constructing strategies under a wide range of parameter values are isomorphic under fecundity and mortality construction. Hence, niches that reduce mortality and those that increase rates of reproduction can be ecologically equivalent with respect to niche construction.

2. Species investing in fecundity construction are able to competitively exclude others when their relative competitive advantage over a another species is greater than the ratio of the species resource use. Thus, i will outcompete j when $b_{ij} > U_j / U_i$.

3. When different species can extract differential benefits from a "single" niche, then coexistence of species with different levels of niche construction becomes possible.

4. Without niche monopolies, there is no niche construction, and $c \rightarrow 1$.

5. When we allow for monopolization, the optimal level of niche construction is at an intermediate level, with energy distributed between reproduction and niche construction. The level of construction for a given value of m is dependent on individual replication rates within a species and death rates. Individuals evolve niche construction to a stable level $(1 + m\lambda/r)/(1 + m)$. When the niche is perfectly monopolized, the level of niche construction is given by $1/2 + \lambda/2r$. Thus, longer-lived species (low value of λ) will tend to invest more in niche construction than will short-lived species.

6. Each species evolves toward a different level of niche construction dependent on a variety of species-specific parameters, including reproduction rates, death rates, com-

petitive ability, and the efficiency of niche exploitation. For all species, the level of niche construction increases with death rate, exploitation efficiency, and the reduction in density due to competition. To the extent that populations within species are characterized by differences in these parameters, one might also expect differences in levels of niche construction among demes.

7. The stable level of niche construction evolving under sympatric competition is strongly influenced by birth and death rates and is lower than the level that evolves in allopatry.

Discussion

Niche construction has been referred to as a "neglected process in evolution" (Odling-Smee et al. 2003) because the environment and the organism have typically been treated as time-separable dynamical systems, while their reciprocal interactions have been neglected. We refer to this situation as "adiabatic evolution" in analogy with thermodynamics, where an adiabatic process is one isolated from its thermal environment through a separation of timescales. When traits of a phenotype capable of modifying the environment of an organism are considered and timescales overlap (niche construction), then selection pressures can be seen, in part, to be encoded in the organismal genome (Dawkins 1978; Lewontin 1982; Odling-Smee et al. 2003). This introduces a circular causality into evolutionary dynamics, with implications for the evolution of development, sociality, and long-term macroevolutionary patterns. Furthermore, environments possess many causally significant variables, and we might expect niche construction to involve a diverse suite of mechanisms for modifying or constructing different environmental variables. Here we present a theoretical approach to niche construction that attempts to capture both the implications of a detailed mechanism and a few generic evolutionary constraints.

We introduce three functional classes of niche-construction mechanisms: mechanisms that construct physical factors modulating the carrying capacity, mechanisms that construct factors incrementing fecundity, and mechanisms that construct factors diminishing mortality. Each construction mechanism introduces new dimensions and timescales into the population dynamics of a multispecies ecosystem. However, all mechanisms face the same construction dilemma, whereby trade-offs between reproduction and niche construction, such as those suggested for corals and birds, for example (Rinkevich 1996; de Neve and Soler 2002; Moller 2006), can lead to niche-construction strategies becoming competitively excluded.

We have sought to characterize the conditions and mechanisms under which we expect niche construction to be viable. We find that the ability to monopolize some fraction of the shared niche is essential for niche construction to evolve. Furthermore, individuals in a stable niche-constructing steady state can adopt a range of different constructive strategies, leading to diversity in the relative investment in reproduction and construction. This can have the appearance of reproductive altruism, but it requires none of its assumptions. In the following subsections, we discuss the implications of both diversity in niche-construction mechanisms and the construction dilemma for issues of stability or robustness, the division of labor, behavioral switches, and macroevolutionary patterns.

Niche-Constructing Robustness and Endogenizing the Carrying Capacity

An immediate consequence of niche construction is the reduction of sensitivity to fluctuating, environmentally determined variables. Whereas those species that depend on processes out of their own control can be eliminated following disturbance, niche construction introduces greater autonomy into the life cycle (Krakauer and Zanotto 2009). Niche construction provides a buffer against environmental fluctuations by increasing population densities and reducing dependencies on uncertain environmental resources. We have not modeled niche construction using stochastic methods and so consider fluctuations to be any changes in population density of sufficient magnitude to destabilize a steady state. We have treated external inputs into the niche through a combination of abiotic process and an "ecosystem-engineered" parameter p. The rate of niche decay is modeled as the product dz. Without niche construction, the steady state niche reaches a resource level p/d and a species density $k_y p/d$. Hence, the number of individuals that a niche can support declines the shorter the half-life of the niche ($1/d$). Perturbations of a given magnitude will have a proportionally greater impact in a rapidly decaying niche—a niche with a lower rate of ecological-niche inheritance—all else being equal.

Consider the following example. The evolution of bird nests is assumed to have originated in simple burrowing behavior (Winkler and Sheldon 1993). In the *Hirundinidae* (swallow) species, nest construction is particularly diverse, yet the construction of mud nests seems to trace to a single ancestral innovation in behavior associated with the construction of such nests in dry conditions in Africa. The construction of nests is hypothesized to have been favored in poor conditions that restricted access to burrows. When mud nests were constructed, a sequence of new social behaviors were facilitated that were precluded in the ancestral condition (Winkler and Sheldon 1993). In the *Agapornis* parrot, the evolution of the ability to construct

domed nests has been associated with colonial breeding, where nests within cavities allow breeding pairs to make use of formerly unsuitable cavities to rear young (Eberhard 1998). In both cases, consistent with the implications of competitive niche-construction theory, harsh environmental conditions favor the evolution of niche construction.

The nest building behavior of the termite represents a strong example of endogenizing carrying capacities. For termites, niche construction is very rich and should be thought of as extending to the agricultural cultivation of the symbiotic occupants of the nest, the mutualistic fungi. In the genus *Termitomyces* of macrotermitine termites, the domestication of fungi in nests is thought to have occurred once, leading to termites becoming one of the major decomposers in the Old World tropics (Aanen et al. 2002).

An important implication of the increased robustness of niche-constructing populations is that the carrying capacity, a somewhat ill-defined component of density regulation, becomes a physiological, behavioral, or metabolic characteristic of an organism capable of extracting essential resources from the environment. Carrying capacity becomes a variable of a population or a species rather than a fixed value. Among the critical lacuna of the current understanding of the growth of biodiversity is that carrying capacities are treated as fixed values. We have sought to "endogenize" carrying capacity (in the sense of economic theory) so that carrying capacity is treated as a dynamic variable.

The Division of Labor

We find that, within a population, different lineages can assume different levels of investment in niche construction. This variation in construction arises through variation in critical life-history parameters. In terms of our models, this amounts to observing some subset of the population that is dedicated to greater investment in reproduction and another subset that is dedicated to niche construction. In the fecundity model, differences in death rates or birth rates between species translate into differences in stable levels of niche construction in the coexistence regime.

Typically, stable polymorphism in the level of investment in reproduction or construction—for example, into germ cells or somatic cells within a population—elicits an explanation in terms of kin selection or group selection. Here we show that diminished reproduction need not imply reproductive altruism but an alternative life-history strategy, with equal fitness sustained across the population through the systemic benefits provided by the niche. An advantage of the niche-construction interpretation of reproductive polymorphism is that it can operate on populations that are completely unrelated: they need only be coupled through their mutual dependence on a partially monopolizable niche. This applies even when the species are engaged in active competition over the niche. All that we require is that niche benefits, not necessarily in equal proportion, are available to all competitors.

This raises many questions and perhaps challenges some important assumptions about the origins of sociality, in particular where we observe a division of labor. The almost complete absence of kin recognition among the social spiders is a case in point. Social spiders do not resist the introduction of unrelated individuals into family-based groups and hence do not achieve group closure (Pasquet et al. 1997). This leads to a situation where individuals of uncertain relatedness can contribute differentially to the construction and maintenance of a partially shared niche, which often extends to cooperating in prey capture and caring for egg sacs and juveniles. It has been suggested that high levels of inbreeding or limited dispersal from a founding colony (Aviles 1986) might elevate the average relatedness in a population to a level where discrimination becomes difficult or unnecessary. There is some evidence for discrimination in the social crab spider *Diaea ergandos* (Evans 1999) following food shortages, whereon nonkin are preferably consumed. This is the only documented example of kin recognition in this group. Our results suggest an alternative possibility. Variation in niche-construction-related behavior is not a problem that requires mechanisms of kin recognition and nepotism, but it can be desirable in conditions of partial niche monopoly. Differential niche construction can maximize the productivity of all members of a group, raising the effective carrying capacity and fecundity of all group members in equilibrium.

The Evolution of Development

The assumption of an absolute trade-off between niche construction and all features of reproduction to include development is a strong constraint, and it is likely to be relaxed in many species. Development is often intimately involved in the construction of the niche of a species and in contributing to the ecological inheritance of a population. Consider the development of an oyster or a reef-building Cretaceous rudist bivalve. Shell secretion is an essential part of development, but the accumulation of shells changes the local current patterns and produces attachment surfaces for future generations. A better way to think about development in relation to niche construction is to treat development as the construction of a somatic niche and the subsequent phenotypes as perfectly monopolizable, spatially localized resource vectors. The degree of control over a niche is dealt with in our formalisms

through the parameter *m*, which we might think of in this context as modulating how development-like an ecological process appears.

It is a topic for future research to allow the extent of the monopoly to vary among strains/species and to explore the conditions under which variably monopolizable niches evolve. One immediate consequence of our results is that monopolies eradicate the construction dilemma. By limiting access to a constructed niche, the level of investment in the niche can be greatly increased. This has obvious implications for the comparative complexity of bodies in comparison with most animal societies. Bodies have as a defining characteristic the funneling of the majority of resources garnered from the environment back into their own germ lines. The evolution of development is thereby rendered as a special case of the division of labor through differential niche construction. In much the same way nests and webs can be thought of as "extended phenotypes" (Dawkins 1978), we can think of phenotypes as abbreviated or contracted ecosystems.

Facultative Strategies

An ability to switch rapidly from an investment in niche construction to reproduction provides a significant competitive benefit. As a consequence of the construction dilemma, when monopolies are not possible, niche construction should be reduced and, when possible, niche construction restored. Furthermore, under many different niche-constructing scenarios, we find that the optimal level of niche construction is a function of a number of organismal and environmental parameters. For example, with fecundity construction and $m = 1$, the selected value of c_x is $1/2 + \lambda_x/2r_x$. Factors contributing to an increase in the death rate λ_x or to a reduction in the rate of reproduction r_x will select for reduced rates of niche construction. These parameters are known to vary over the course of a lifetime and with different conditions of sociality. Typically, there is a trend toward larger values of λ_x and smaller values of r_x with age, and the reverse trend is observed when considering the level of sociality.

The influence of potential increases in death rates on niche construction has been studied in the St. Andrew's Cross spider *Argiope versicolor*. This spider is preyed on by the jumping spider *Portia labiata*. When exposed to a range of predator cues, juveniles of *A. versicolor* decreased the frequency of web building and refrained from consolidating the existing web area and capture area and from building capture silk threads, compared with a blank control and a nonpredator control (Li and Lee 2004).

We might also ask whether species have evolved facultative niche construction under conditions of recurrent, competitive equilibrium. Behavioral plasticity and learning have been shown to be effective strategies (above and beyond mutation and selection) when environments change over short timescales relative to ontogeny (West-Eberhard 2003). Similarly, phenotypic plasticity is an effective response to environmental variability over slightly longer timescales. Environmental change that has an impact on key life-history parameters can shift populations from coexistence into competitive regimes, each favoring different levels of niche construction. For example, termites show ontogenetic switches between foraging and mound building, and population size—which is likely to influence death rates—has been discussed as a factor in this switch (Evans 2006).

Macroevolutionary Ratchets

The slow timescale of niche decay can promote niche inheritance whereby several generations of individuals contribute to and exploit a single niche. This leads to the possibility of multiple rounds of niche construction generating directional trends in niche size and abundance. Over macroevolutionary timescales, such feedback appears to have progressively increased the extent of shell beds (as discussed in the previous subsection on development), of bioturbation of shallow marine sediments by burrowing and bulldozing marine invertebrates, and, in some aspects, of the response of prey to increased predation (Erwin 2008). It seems quite likely that the extent of niche construction has increased over time, coincident with more effective niche monopolies. In these models, we have placed a ceiling on the maximal, absolute value of a niche because the niche is ultimately limited by resource availability. If we allow for the possibility of sequential niche construction by different sets of species, such an accumulative outcome could be generated.

Although these models were not designed to address the role of niche construction through long periods of evolution, particularly over macroevolutionary timescales, several interesting implications are suggested by our results. For example, the conclusion that, for fecundity- and mortality-related niche construction, longer-lived species are more likely to invest in niche construction could provide new insights into life-history strategies of a variety of groups. If it also proves to be true that species with longer durations are more likely to construct niches, then it is suggested that the apparent long-term decrease in short-lived marine taxa (Jablonski and Flessa 1986) may reflect an overall long-term increase in niche construction.

The Future

The results of these models suggest several promising directions for further research. One of the assumptions in

these models is that energy and time invested in niche construction is subtracted from energy and time invested in replication. But niche construction activities can increase the total energy available to individuals of a species as well as the species as a whole, enhancing the energy devoted to development, reproduction, and niche construction. Certainly over evolutionary timescales, niche construction appears not to have been a zero-sum process and has contributed, probably substantially, to increased diversity.

We have largely neglected the effects of ecosystem engineering (Jones et al. 1994), where the activities of organisms have significant spillover effects on other species. We treated those species extrinsic to niche construction dynamics through the parameter p. The relationship between niche construction and ecosystem engineering is a complex one, particularly in evolutionary time where reliably identifying the fitness effects of niche construction (sensu stricto) can be difficult. Analyzing these effects requires a system with multiple niches and with diffuse contributions across species occupying different niches. In this way, we might identify when niche construction by one species becomes ecosystem engineering for another.

Another interesting avenue to explore is the effect of occasional disturbance. The results of the first set of models demonstrate that when there are trade-offs between niche construction and reproduction, niche construction persists provided that niches can be monopolized. But these results do not consider disturbances. If disturbance leads to the extension of the competitive phase, it is predicted to induce a shift toward investment in reproduction. If so, the frequency and magnitude of disturbance faced by a population could moderate the trend toward increased investment in niche construction. The conclusion that only one species can persist in a niche over the long term may not apply if disturbances occur more frequently than the time taken to achieve competitive exclusion. Finally, it will be interesting to explore whether such models have implications for the relative investment in niche construction after mass extinctions and other biotic crises.

By considering a diversity of niche-construction mechanisms, we have been able to show how different "environmental" properties are more or less likely to be constructed by organisms, and we determined their stability properties. However, the dynamics of the construction process and the dynamics of the niche itself remain very simple. Of obvious interest is to consider how we might include details of behavioral sequences leading to the construction of niches and their relationship to the cognitive capacities of species. Niches, once constructed, necessarily interact with other niches and are likely to contribute directly to the construction of further niches. This will be an important consideration when extending these ideas to "cultural artifacts" that are invariably used in subsequent embedded construction algorithms.

Literature Cited

Aanen, D. K., P. Eggleton, C. Rouland-Lefevre, T. Guldberg-Froslev, S. Rosendahl, and J. J. Boomsma. 2002. The evolution of fungus-growing termites and their mutualistic fungal symbionts. Proceedings of the National Academy of Sciences of the USA 99: 14887–14892, doi:10.1073/pnas.222313099.

Aviles, L. 1986. Sex-ratio bias and possible group selection in the social spider anelosimus eximius. American Naturalist 128:1–12.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416:427–430, doi: 10.1038/416427a.

Dawkins, R. 1978. Replicator selection and the extended phenotype. Zeitschrift für Tierpsychologie 47:61–76.

de Neve, L., and J. Soler. 2002. Nest building activity and laying date influence female reproductive investment in magpies: an experimental study. Animal Behaviour 63:975–980.

Eberhard, J. 1998. Evolution of nest-building behavior in agapornis parrots. Auk 115:455–464.

Elton, C. (1927) 2001. Animal ecology. University of Chicago Press, Chicago.

Erwin, D. H. 2008. Macroevolution of ecosystem engineering, niche construction and diversity. Trends in Ecology & Evolution 23:304–310.

Evans, T. 1999. Kin recognition in a social spider. Proceedings of the Royal Society B: Biological Sciences 266:287–292.

———. 2006. Foraging and building in subterranean termites: task switchers or reserve labourers? Insectes Sociaux 53:56–64.

Grinnell, J. 1917. The niche-relationships of the California thrasher. Auk 34:427–433.

Gurney, W., and J. Lawton. 1996. The population dynamics of ecosystem engineers. Oikos 76:273–283.

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

Jablonski, D., and K. Flessa. 1986. The taxonomic structure of shallow-water marine faunas: implications for phanerozoic extinctions. Malacologia 27:43–66.

Jones, C., J. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

———. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Krakauer, D., and P. Zanotto. 2009. Viral individuality and limitations of the life concept. Pages 513–536 *in* S. Rasmussen, M. Bedau, L. Chen, D. Deamer, D. Krakauer, N. H. Packard, and P. F. Stadler, eds. Protocells: bridging non-living to living matter. MIT Press, Cambridge, MA.

Laland, K., F. Odling-Smee, and M. Feldman. 1996. The evolutionary consequences of niche construction: a theoretical investigation using two-locus theory. Journal of Evolutionary Biology 9:293–316.

Lewontin, R. C. 1982. Organism and environment. *In* H. C. Plotkin, ed. Learning, development and culture. Wiley, New York.

Li, D., and W. Lee. 2004. Predator-induced plasticity in web-building behaviour. Animal Behaviour 67:309–318.

Moller, A. 2006. Rapid change in nest size of a bird related to change in a secondary sexual character. Behavioral Ecology 17:108–116.

Odling-Smee, F., K. Laland, and M. Feldman. 2003. Niche construction: the neglected process in evolution. Princeton University Press, Princeton, NJ.

Pasquet, A., M. Trabalon, A. Bagnères, and R. Leborgne. 1997. Does group closure exist in the social spider *Anelosimus eximius*? behavioural and chemical approach. Insectes Sociaux 44:159–169.

Rinkevich, B. 1996. Do reproduction and regeneration in damaged corals compete for energy allocation? Marine Ecology Progress Series. Oldendorf 143:297–302.

Schoener, T. 1989. The ecological niche. Pages 79–113 *in* A. R. E. Sinclair and J. M. Cherrett, eds. Ecological concepts. Blackwell Scientific, Oxford.

Silver, M., and E. D. Paolo. 2006. Spatial effects favour the evolution of niche construction. Theoretical Population Biology 70:387–400, doi:10.1016/j.tpb.2006.08.003.

West-Eberhard, M. J. 2003. Developmental plasticity and evolution. Oxford University Press, Oxford.

Winkler, D. W., and F. H. Sheldon. 1993. Evolution of nest construction in swallows (Hirundinidae): a molecular phylogenetic perspective. Proceedings of the National Academy of Sciences of the USA 90:5705–5707.

Wright, J. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56: 203–209.