proach to using butterflies as model systems. They synthesize the findings presented in the chapters of the book and identify several areas of research where butterflies as models could yield useful and generalizable results.

Butterflies can thus be an important model system, but I don't think we should all drop our favorite study system and rush head-over-heels to study butterflies instead. The great diversity of life entails a great diversity of strategies to stay alive. Studying just one group will not lead to a greater understanding of the whole. We cannot distinguish the generalities from the peculiarities, if we have no idea of how things work in other groups of organisms. Let us continue to look at the harsh burden of diversity with enthusiastic eyes and publish our studies in folly! Vivé la diversité!

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Ecology, 85(3), 2004, pp. 880–882

NICHES: LOOKING BACKWARDS, LOOKING FORWARDS

Chase, Jonathan M., and Mathew A. Liebold. 2003. **Ecological niches: linking classical and contemporary approaches.** Interspecific Interactions. The University of Chicago Press, Chicago, Illinois. ix + 212 p. $50.00 (cloth), ISBN: 0-226-10179-7 (alk. paper); $20.00 (paper), ISBN: 0-226-10180-0 (alk. paper).

Odling-Smee, F. John, Kevin N. Laland, and Marcus W. Feldman. 2003. **Niche construction: the neglected process in evolution.** Monographs in Population Biology. Number 37. Princeton University Press, Princeton, New Jersey. xii + 472 p. $75.00, £49.95 (cloth), ISBN: 0-691-04438-4 (alk. paper); $39.50, £26.95 (paper), ISBN: 0-691-04437-6 (alk. paper).

The niche is one of the most enduring concepts and organizing principles in ecology. It is discussed at length and used throughout virtually all textbooks in ecology and environmental science. It is the focus of six (15%) of the papers and lurks in the background of the majority of the others in Leslie A. Real and James H. Brown's *Foundations of ecology* compendium (1991. The University of Chicago Press, Chicago, Illinois). And because Dr. Seuss immortalized it in a familiar 1955 lyric, the niche has penetrated the popular imagination and grounds the general perception that nature is in balance and every species has in its own part in maintaining that balance.

In recent years, however, the niche has lost its luster among ecologists. After years of measuring niche breadth and estimating niche axes, many ecologists began to wonder if they could ever grasp or even graph Hutchinson's *n*-dimensional hypervolume. By the mid-1980s, graduate students were being discouraged from using, much less measuring, niches in their theses and dissertations. Chase and Liebold illustrate a 20-year decline in the percentage of articles in *Ecology* that include the word "niche," and the rate of decline since 1980 is approximately equal in magnitude to the rate of increase from 1960–1980. Has the niche finally run its course as a useful organizing principle for ecologists? According to these two books, both published within the last six months, the answer is an emphatic "No!"

Jonathan Chase and Mathew Liebold (henceforth C&L) argue that the niche, as they re-envision it, can provide deep insights and conceptual syntheses for almost any ecologically interesting situation. In a relatively short book, they redefine and reconstruct the ecological niche; derive new questions and research directions from their niche concept; and identify key challenges that lie ahead as the niche is reincorporated into ecological thought.

The niche, according to C&L, is "the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita impacts of that species on these environmental conditions." This definition is firmly grounded in standard differential equation models for per capita effects of one species on another via competition for shared resources, although they extend these to models for apparent competition via shared predators, and the effects of keystone predators. The mathematics is kept to a minimum—all the equations are confined to an Appendix to Chapter 2—as models and hypotheses are presented throughout the book as phase-plane diagrams of zero net-growth isoclines (or ZNGIs).

The ZNGI framework, developed thoroughly by Tilman in the 1980s is well suited to C&L's approach. Familiar concepts such as the fundamental and realized niche are folded in easily by C&L into the ZNGIs: "[t]he fundamental niche. . . [is] where the supply point of two resources is above the ZNGI. The realized niche. . . is narrower than the fundamental niche. . . because [a species is] competitively excluded from a portion of the range of resources."

The first innovation in C&L's concept of the niche is the replacement of Tilman's "consumption vector"—the impact of a consumer on a resource—with an "impact vector"—the impact of a species on a factor. Thus, a consumer may have a negative impact on its resource, or a prey species may have a positive impact on its predator. The remainder of the book is replete with phase-plane diagrams, multiple ZNGIs, and swarms of impact vectors that arise from applying impact vector analysis to ecological issues such as predator-prey interactions; environmental heterogeneity; succession, assembly rules, and large-scale patterns of diversity; and ecosystem dynamics. For all of these, the fundamental questions are how and under what conditions can species co-exist, and how is this co-existence determined by their niche relationships?

The second innovation in C&L's approach to the niche is their requirement that to be useful, niche axes must be able to be measured. C&L argue that what they refer to as classical niche theory (i.e., everything before C&L) collapsed a large number of quantifiable resource axes into a single niche axis (e.g., a "seed size" or "habitat" niche) for mathematical convenience. Investigators then spent too much time measuring the unmeasurable. In contrast each of C&L's niche axes—"a quantitative measure of an environmental factor"—can be mapped directly onto an axis of Hutchinson's n-dimensional hypervolume. However, despite the wealth of graphical hypotheses, C&L present scant data, suggesting that true measurements of niche axes and solid empirical tests of the consequences of their reformulated niche are still in the future.

Ecological niches is rooted firmly in classical ecological theory (Lotka-Volterra equations, ZNGIs, competition, predation, and succession), and is an excellent synthesis into a coherent framework of the last century's thinking about niches. One of the central tenets of classical niche theory that is retained in C&L is the notion that the environment defines a species' niche, but that the species has no effect (beyond consumption) on its environment. This notion is encapsulated by C&L when they show no impact vector of a species on abiotic "stress." Ecosystem "engineers" modify habitat characteristics (and perhaps ameliorate abiotic stress), but C&L consider ecosystem engineers only briefly, and only in the context of one species indirectly modifying the resource base of another species via engineering activities.

At the same time that C&L were reworking classical niche theory, F. John Odling-Smee, Kevin Laland, and Marcus Feldman (hereafter OL&F) were focusing on how organisms directly modify their environment, and describing the profound evolutionary consequences attendant to this modification, which they term "niche construction." In OL&F's terms, niche construction is the process by which organisms (phenotypes) "modify at least some of the natural selection pressures present in their own, and in each other's, local environments." The subject of OL&F's dense monograph, *Niche construction,* is to explore the evolutionary, and to a lesser extent, the ecological consequences of niche construction.

A brief review cannot do justice to the excitement that OL&F generate with their ideas. The relatively simple observation that at least some, if not most organisms modify their environment is shown by OL&F to have dramatic consequences for our understanding of evolution by natural selection. The standard model of evolution is that organisms transmit genes from generation to generation, and natural selection acts on the phenotypes. This is a one-way street: the "environment" is the selective agent and the organism responds to this selective environment. This one-way street is directly analogous to the absence of impact vectors relating species to abiotic stress in C&L. Niche construction makes this a two-way street and creates a species-environment impact vector: because organisms modify their own (local) environments, each generation not only inherits a genetic legacy from its parents but also inherits a legacy of selection pressures that have been modified by the actions of previous generations on the environment. OL&F call this "ecological inheritance" and they spend nearly 475 pages showing what happens to classical population genetic and evolutionary models when ecological inheritance through niche construction is incorporated.

In essence, OL&F have formalized an idea sketched 20 years ago by Richard C. Lewontin (1983. Gene, organism, and environment. Pages 273–285 *in* D. S. Bendall, editor. *Evolution from molecules to men.* Cambridge University Press, Cambridge, England). Classical evolutionary models can be represented as a pair of coupled differential equations:

$$\frac{dO}{dt} = f(O, E) \qquad \frac{dE}{dt} = g(E)$$

In this formalization, evolutionary (temporal) changes in organisms (O) are a function of both organisms and their environment (E), but temporal changes in environment is a function only of the environment. In contrast, the existence of niche construction changes these coupled differential equations to:

$$\frac{dO}{dt} = f(O, E) \qquad \frac{dE}{dt} = g(O, E)$$

What happens to evolutionary changes in organisms when temporal changes in the environment are a function both of past environments *and* of the actions of organisms?

Three areas are of paramount concern to OL&F. First, if organisms evolve because of selection pressures that can be modified by the organisms themselves, there is feedback in the system. Current evolutionary theory does not incorporate such feedback, yet it can lead to changes in evolutionary rates, fixation of otherwise deleterious alleles, elimination or support for stable genetic polymorphisms, and changes in levels of genetic linkage disequilibrium.

Second, ecological inheritance generates unexpected evolutionary dynamics, including temporal lags in, opposing responses to, and catastrophic responses in the face of selective pressures. Lastly, niche construction has the potential to allow acquired characteristics to influence evolution, albeit without the invocation of Lamarckian inheritance.

Last, the evolutionary consequences of niche construction play out in the ecological theatre. Specifically, niche constructors as ecosystem engineers control, in whole or in part, the flow of energy, materials, and information through local ecosystems. OL&F coin the term "environmentally mediated genotypic associations (EMGAs)" to describe the outcome of different populations interacting with each other through phenotypically manipulated biotic and abiotic components in their environment. Feedback and interactions of EMGAs may influence coevolutionary dynamics, competitive interactions, and ecosystem fluxes.

Niche construction is a thorough exploration of the ecological and evolutionary consequences of organism-environment feedbacks. After a readable introduction, OL&F assemble a large number of examples of niche construction that are grouped into four categories. Organisms can change their environment by perturbing it or by relocating to a better environment. These changes can be initiated by the organism itself (what OL&F refer to as "inceptive niche construction") or organisms can oppose on-going environmental change by modifying the environment ("counteractive niche construction"). Perturbation and relocation on the one hand, and inceptive and counteractive niche construction on the other are orthogonal categories, and give rise to four categories of niche construction (inceptive-perturbation; inceptive-relocation, etc.). Lastly, niche construction can either be positive and result in an environment that increases the average fitness of the niche constructor or be negative and result in an environment that reduces the average fitness of the niche constructor. OL&F assert that niche construction is universal, and although some of their examples may seem far-fetched, the unavoidable conclusion from their convincing work is that niche construction indeed is ubiquitous and evolutionary models must incorporate organism-environment feedbacks.

Like C&L, OL&F present their models graphically and relegate the formal mathematics to a series of appendices. Models are developed for selection on niche constructors that are randomly mating diploids with two diallelic loci interacting with a single resource, haplo-diploids, or diploids with sex-linked loci. The models are extended to complex resource dynamics, cultural inheritance, and evolution of sex-ratios. Each of these models gets its own chapter that clearly explores their outcomes. A particularly useful set of chapters presents predictions of these models for evolutionary dynamics, for ecological processes, and for humans.

What is especially appealing is that the niche construction framework overcomes many of the objections to classical sociobiology. While it may have been socially acceptable to view non-human organisms simply as packets of genes, viewing humans through a classical evolutionary lens led to much acrimony. In contrast, OL&F re-integrate humans into the evolutionary play by extending organism-environment feedbacks to all organisms, including humans (for whom niche constructing activities, both positive and negative, are on constant display).

These two books are a study in contrasts. *Ecological niches* is firmly grounded in classical ecology and reinvents the niche in a way that most ecologists will find comfortable and that will require little reorientation of ecological research programs. *Niche construction* takes off from standard population genetics theory, but reinvents both the niche and evolutionary theory in ways that require a revolutionary re-thinking of ecological and evolutionary dynamics. In short, if you want to see where niches came from, read *Ecological niches.* If you want to see where they're going, read *Niche construction.*

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Ecology, 85(3), 2004, pp. 882–883

WESTERN BIRDS AND HABITAT FRAGMENTATION

George, T. Luke, and David S. Dobkin, editors. 2002. **Effects of habitat fragmentation on birds in Western landscapes: contrasts with paradigms from the eastern United States.** Studies in Avian Biology. Number 25. Cooper Ornithological Society, Camarillo, California. 270 p. $35.00 (cloth), $22.00 (paper), ISBN: 1-891276-34-4.

Effects of habitat fragmentation on birds in Western landscapes: contrasts with paradigms from the eastern United States, edited by T. L. George and D. S. Dobkin, fills some of the gaps in our knowledge about the consequences of habitat fragmentation for bird populations of the western United States. The book pushes readers to expand the sometimes-myopic view of fragmentation as deciduous woodlots surrounded by cornfields to a broader perspective that includes old-growth coniferous forests fragmented by regenerating forest, chaparral patches surrounded by residential development, and shrubsteppe vegetation fragmented by expanses of exotic grasses.

After the editors' introduction, the first of three sections includes seven papers that address issues related to avian responses to fragmentation. Thompson et al. provide a conceptual framework for understanding fragmentation effects on birds as understood by researchers working in the eastern United States. Definitions and methodological issues related to fragmentation are addressed by Franklin et al. and Sisk and Battin. Several of the papers review work on fragmentation-related issues such as edge effects, cowbird abundance, and nest predation in an east vs. west context (Sisk and Battin, Morrison and Hahn, Cavitt and Martin, respectively) and/or provide new analyses of data collected over large geographical areas (Cavitt and Martin, and Hames et al). The paper by Kotliar et al. contains useful information on the responses of bird communities to fire but its contribution to this volume with its focus on fragmentation was marginal.

The six papers in the second section examine new data and review previous work on bird distributions, abundances, and nesting success in particular patch and matrix vegetation types in the western United States, including mature coniferous forests within regenerating coniferous forest (George and Brand, Manuwal and Manuwal, Hejl et al.), shrublands within grasslands dominated by exotic species (Knick and Rotenberry) or residential development (Bolger), and decid-