ing a substantive claim about the world in the same way that the law of inertia does. It can be proven mathematically; it does not need to be tested.

Even granting McShea and Brandon's claim that the ZFEL is a law, the question remains whether it is a zero-force law. Recall the leaf-blowing thought experiment. Is that really a zero-force state? We might have taken the wind to constitute a force acting on the leaves, but the authors seem to suggest that we should not count it as a force because it is not directional. This appears to me to be splitting hairs: If not a force in that technical sense, the wind is surely a cause, one that influences the various locations of the leaves. (And in the book McShea and Brandon give every reason to think they would see the wind as a cause.) In the ZFEL, new variation arising randomly plays the role of the wind. To cite one of the authors' many examples, if we had a number of populations of the same species in different environments, each undergoing natural selection in different ways, there would be a tendency (in the absence of constraints) for the populations to diverge from one another. The variations introduced into each population from the different selection pressures would be "random with respect to each other" and thus satisfy that criterion of the ZFEL. But surely these are different causes acting, with the unsurprising result that different effects occur. It is not clear why these causes would be any different in status from the causes acting in a situation where each population were in a similar environment, each undergoing natural selection in a similar way. There is no reason to think that the situation where the populations are undergoing natural selection in different ways is more fundamental, or more of a "zero-force" state, than the situation in which they are undergoing natural selection in the same way. And once we acknowledge that, it becomes even more unclear why certain causes (namely, random variation and heredity) are considered to be an omnipresent background, whereas other causes are picked out as constraints or forces acting against a "spontaneous" (McShea and Brandon's term) tendency.

What happens, then, if (in spite of its name) the ZFEL isn't really a zero-force law at all? The authors' generalization loses some of its rhetorical punch, perhaps, but punch isn't everything. There is a very interesting question lurking beneath the rhetoric of zero-force law (and, sadly, it risks being overshadowed by that rhetoric): Considering every level of the biological hierarchy, how prevalent are biological systems that satisfy the assumptions of the ZFEL—namely, heredity and random variation—with or without constraints or countervailing forces? If the answer turns out to be "most" or even "many," then McShea and Brandon will have drawn our attention to a widely applicable generalization that was known in particular cases without us necessarily having seen the forest for the trees. And even if the answer turns out to be "few," it still means that in each case we will have to consider whether we need to invoke special explanations for observed increases in diversity over time. A generalization does not have be a zero-force law, or a law at all, in order to be important, useful, and informative.

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ECOLOGY

Why a Grand Unified Theory Is Neither Feasible nor Desirable

Tadashi Fukami

Ecology as a scientific discipline struggles with the dilemma of generality versus specificity. Robert MacArthur, a founder of modern ecology, reminded us that "Science should be general in its principles" (*1*). But many researchers, presumably including MacArthur himself, have been drawn to the discipline because of a fascination with the diversity of organisms and ecosystems. We love to learn the unique details of ecological phenomena. Of course, a widely recognized problem of working with a specific focus is that it prevents us from seeing the grand scheme of how nature works, which can in turn limit our understanding of details.

From Populations to Ecosystems
Theoretical Foundations for a New Ecological Synthesis
by Michel Loreau
Princeton University Press, Princeton, NJ, 2010. 316 pp. $99.50, £69.95. ISBN 9780691122694. Paper, $45, £30.95. ISBN 9780691122700. Monographs in Population Biology, 46.

This problem is relevant not only to organisms or ecosystems but also to specific subdisciplines, each concerned with a particular

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Bridging subdisciplines. Loreau offers a theoretical framework for linking population biology, community ecology, and ecosystem analysis.

level of biological organization (from populations to communities to ecosystems). It presents a challenge to the many who are searching for overarching principles that would meld the subfields. Attempts to develop unified general theories have proliferated in the ecological literature in recent years. But how general is general enough? If the utility of a general theory is determined by its level of generality, then the more general the better—with the ultimate goal being the formation of a single overarching ecological theory. However, the attendant simplification that comes with generalization forces us to ignore the very details about organisms and ecosystems that drew us to ecology in the first place.

A recent addition to the Monographs in Population Biology series [which began in 1967 with a contribution from MacArthur and E. O. Wilson (*2*)] powerfully presents one solution to this persistent dilemma. In *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*, Michel Loreau argues that an effective way forward is to give up building a single unified theory of ecology altogether. Loreau (a theoretical ecologist at McGill University) believes that "a monolithic unified theory of ecology is neither feasible nor desirable." As an alternative approach, he advocates theoretical merging of closely related, yet separately developed subdisciplines.

The merging (or bridge-laying) Loreau advocates involves translating different "languages" used in the mathematical models developed separately in various subdisciplines into a common language so that the subfields can talk to one another. Although this approach does not yield a truly unified theory, it helps, Loreau argues, to "generate new principles, perspectives, and questions at the interface between different subdisciplines and thereby contribute to the emergence of a new ecological synthesis that transcends traditional boundaries." Taking this tack, one gets a sense that the problem with specialization in subdisciplines can be solved by theoretical bridging without having to trade specificity for generality.

An elegant example of the author's approach can be seen in the work conducted by him and his colleagues over the past decade or so that merges two major subdisciplines of ecology, community ecology and ecosystem ecology. Loreau devotes much of the book to recounting this body of research. He starts by summarizing essential elements of the mathematical models developed in the two subdisciplines. He then discusses how the two sets of models, though developed separately and with apparently distinct sets of equations, can be merged by basing the two on a common currency: the mass and energy budgets of individual organisms. Once this translation is accomplished, new models that simultaneously consider the composition of coexisting species (the focus of traditional community ecology) and the flow of materials through functional compartments of ecosystems (the focus of traditional ecosystem ecology) can be built and analyzed. These allow one to study reciprocal influences between species composition and material flows in the ecosystem.

As Loreau acknowledges, his is not the first book to advocate this type of theoretical merging. In particular, the approach he presents resembles that laid out in an influential 1992 book by Donald DeAngelis (*3*). What makes Loreau's contribution novel and creative is his successful application of the merging approach to understanding the functional consequences of biodiversity loss, the topic that has received perhaps greater attention than any other ecological issue over the past two decades because of its broad social implications. Loreau's theoretical work has subsequently stimulated empirical investigation of community assembly as a fundamental process underlying the relationship between biodiversity and ecosystem functioning over both ecological (*4*) and evolutionary (*5*) time scales. Although more empirical evidence is needed, Loreau also discusses how similar types of theoretical merging can be useful for linking spatial ecology and evolutionary ecology with the now integrated community-ecosystem ecology. Looking further ahead, he suggests linking ecology more tightly to stoichiometry, genomics, and economics as future research directions that can benefit from more theoretical bridging.

For those readers who expect a truly unified theory of ecology from such ambitious words as "theoretical foundations" and "new ecological synthesis" used in its title, *From Populations to Ecosystems* may be disappointing. Certainly, although not pursued in the book, the ongoing search for greater unified theories should be continued, as it can help us see similarities among disparate systems and levels of organization. It seems likely, however, that ecology is inherently not a discipline in which a single general theory can be developed (*6*), a characteristic that leaves the apparent generality-specificity dilemma unresolved. In this light, Loreau's book demonstrates a valuable approach that eliminates the dilemma to a large extent, opening up exciting new avenues of research.

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