What Hypotheses Are You Willing to Entertain?

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abstract: The 2005 American Society of Naturalists Vice-Presidential Symposium was organized on the theme of "Integrating across Scientific Disciplines." Integration implies considering some aspect of nature from disparate vantages that cut across disciplinary boundaries. The articles presented here illustrate that taking integrative approaches to addressing research questions yields much greater insights than do piecemeal contributions by separate fields.

Ecology and evolutionary biology long ago moved well beyond simply describing the natural world. Ecologists and evolutionary biologists, like all scientists, develop ever more complex theories of how nature works, and these theories guide us in how we examine the real world. Because of our increased understanding of nature's complexity, scientists are forced to become ever more specialized. This specialization is necessary to maintain a deep understanding of the problems and developments in the discipline that each scientist has decided to explore. However, this ever-deepening specialization within disciplinary boundaries necessarily makes our theories more compartmentalized and makes incorporating relevant advances across disciplines more difficult.

The erection of disciplinary boundaries also has consequences more insidious than simply making it harder for everyone to keep up with a literature burgeoning in all directions. Each discipline develops hypotheses and ultimately theories to explain the features of nature on which it focuses. In so doing, decisions must be made as to which mechanisms are directly relevant to the question at hand and which are more peripheral. Predictions are then constructed, based on the actions of those mechanisms deemed relevant, and mechanisms considered to be more peripheral are ignored. These decisions then guide empirical investigations as to which variables to measure and which timescales to consider. Certainly, this is the correct way to do science, given that more peripheral mechanisms are expected to have less influence than those directly acting in a chain of causation. However, in our working life, judgments about which mechanisms to include and which to ignore are frequently based more on our own disciplinary predispositions or simple expedience than on sound biological grounds. Unfortunately, many features of nature are directly influenced by multiple mechanisms that fall into disparate scientific disciplines.

Because the main ways we deal with these issues depend on personal judgment and understanding, I offer one illustration of these issues from my own work on damselflies (Odonata). My research interests center on the processes that shape species richness and diversity patterns of extant biological communities. Having done master's degree work in behavioral ecology, my dissertation work focused on understanding how behavioral differences influence species' coexistence at the community level. In a behavior experiment performed as part of my dissertation work, I showed that *Ischnura* species were much more active than *Enallagma* species in the absence of predators and that *Enallagma* species reduced their activity to a much greater degree in the presence of predators (McPeek 1990, 2004). These differences between the genera are consistent with a trade-off between mortality and growth that is modulated by activity—reduced activity results in reduced mortality from predators, but this reduced mortality comes at the cost of reduced feeding and growth (Lima and Dill 1990; Werner and Anholt 1993; Lima 1998). Such a trade-off mediated by activity is predicted to foster species coexistence, because one group is more successful at predator avoidance, whereas the other group is more successful at competing for available resources (e.g., Levin 1970; Holt et al. 1994; Leibold 1996; McPeek 1996). Based on these predictions, I then performed a series of field experiments and found that *Ischnura* species did indeed grow substantially faster than *Enallagma* species and that *Enallagma* species suffered substantially less mortality from predators than *Ischnura* species—just as predicted by the activity-mediated trade-off (McPeek 1998).

At this point, I thought that I largely understood the mechanisms promoting coexistence between *Enallagma*

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and *Ischnura* damselflies. However, a few results from these experiments were difficult to reconcile with the presumed trade-off. Other field experiments showed that all species were resource limited, but the two genera were completely symmetrical competitors for resources (McPeek 1998), which should not be true if *Ischnura*'s greater activity gives it an advantage at consuming resources. Also, in the laboratory behavior experiment, the *Ischnura* species ate on average less prey than almost all *Enallagma* species, and activity was uncorrelated with feeding rate across species (McPeek 2004). These latter inconsistencies could have been an artifact of a staged laboratory experiment (i.e., not everything will go exactly as you expect), but repeated experiments convinced me that these results were not artifacts.

In fact, the explanation for growth rate differences among these species does not lie within the realm of behavioral ecology at all but rather within physiological ecology. Although species differed dramatically and consistently in short-term (i.e., over minutes) feeding rates, *Enallagma* and *Ischnura* species consumed identical amounts of food in both the presence and absence of predators when measured over days (McPeek 2004); this explains why they are symmetrical resource competitors. Also, when predators were absent, *Enallagma* and *Ischnura* species grew at equivalent rates. However, despite consuming identical amounts of food, *Enallagma* species gained substantially less mass in the presence of predators than did *Ischnura* species (McPeek 2004). Thus, although *Enallagma* and *Ischnura* species differ in many ways that are exactly consistent with the activity-mediated trade-off, their growth rate differences have nothing to do with activity and are in fact caused by physiological responses to the presence of predators that differentially alter their abilities to convert ingested food into their own biomass.

Consider the importance of understanding the mechanism of species interactions in this example. If activity mediated the trade-off between growth and mortality, the two groups should have substantially different impacts on their common resource base, with one able to deplete resources to a much greater degree than the other (e.g., Tilman 1982; Leibold 1996). In contrast, these species show a purely physiological response to predators in which all species have equivalent abilities at depleting resources under all conditions, but they differ in conversion efficiency. Thus, these two mechanisms imply fundamentally different consequences for expected food web dynamics. Moreover, model results suggest that differences in ingestion rate among species tend to promote stable coexistence, whereas differences in conversion efficiency tend to destabilize species interactions (Leibold 1996). Thus, at this point, it still remains unclear whether these differences in growth and mortality among *Ischnura* and *Enallagma* species contribute to their coexistence.

As my experiences highlight, the hypotheses we are willing to entertain critically determine how we see the world and strongly influence our abilities to pursue the correct paths in a research program. Assumptions about the workings of nature accumulate within each scientific discipline, and over time these assumptions can become engrained in the fabric of the discipline. We forget that many of these assumptions were made for reasons other than being supported by sound data and rigorous testing. Thus, continually questioning the fundamental assumptions of a discipline is a major component of advancing that field.

One strong way to do this is to ask what insights are gained by examining the aspect of nature in which you are interested from the perspective of related scientific disciplines. If the conclusions of one discipline are true, we should be able to integrate them with the observations, experimental results, hypotheses, and theories of related disciplines. For example, if the activity-mediated trade-off had primarily governed the interactions among the damselfly species, I would have expected quite different results from those I obtained in my physiology experiments. Moreover, many different disciplines within ecology and evolutionary biology are exploring the same aspects of nature, and so such integration is not only a practical check on the direction of a field's development but also a fundamental requisite of fully understanding that feature of nature. For example, quantitative genetics, molecular biology, and developmental biology are all exploring how a phenotype is constructed and evolves. Community ecology, systematics, paleontology, and conservation biology (to name just a few) are in their own ways all trying to understand patterns of species richness and diversity and the processes that have generated and maintain those patterns. The dynamics of chemical compounds in the environment are central to questions addressed by ecosystem ecologists, forest biologists, limnologists, microbial ecologists, physiological ecologists, and populations biologists. Despite shared goals, the exchange between disciplines is often poor, although examples exist where such exchanges and integration of ideas have been tremendously fruitful (e.g., the emerging field of evolutionary developmental biology—"evo-devo").

In addition to apparent intellectual barriers, many other impediments also offer practical hindrances to integrating across disciplines (Hull 1988). Past training and education give one specific knowledge within a narrow range of disciplines, and this educational background shapes how each individual scientist builds future inquiries. Many career incentives (e.g., publication success, salary raises, promotion and tenure decisions, recognition by awards) tend to reward disciplinary specialization over integration. Scientific meetings are primarily focused on disciplines, and few try to cross boundaries. Department structures in universities and other scientific institutions (e.g., scientific funding agencies) continue to fragment the biological sciences into ever more specialized administrative structures. Finally, advances in one field can raise technical and financial barriers to broadly utilizing those advances outside the discipline (e.g., access to sophisticated equipment and the technical expertise to collect data outside one's own area is often limited more by financial considerations than the motivation to expand one's research program into new areas).

With these issues in mind and because the purpose of the American Society of Naturalists is "to enhance the conceptual unification of the biological sciences" (http://www.amnat.org/abo.html), I decided to organize the 2005 Vice-Presidential Symposium in Fairbanks, Alaska, around the theme of "Integrating across Scientific Disciplines." My goal was to invite a group of scientists whose work exemplifies the best of integrating ideas and approaches across a wide spectrum of biological disciplines and beyond. They were each asked to present some aspects of their work that highlight both the way they integrate across disciplines and the unique conclusions (and sometimes pitfalls) that come from such integration.

The collection of articles presented here illustrate integration of research initiatives that span much of the biological sciences. Paul M. Brakefield's contribution with J. C. Roskam uses evolutionary genetics and evolutionary developmental biology to explore the mechanisms that constrain and bias the paths of possible evolutionary change in the patterns of butterfly wing eyespots. The contribution by Ron S. Burton and colleagues considers how coadaptation between the nuclear and mitochondrial genomes influences physiological performance and organismal fitness to shape patterns of population differentiation and ultimately speciation in an intertidal copepod. James Elser explores how the stoichiometric balance of carbon, nitrogen, and phosphorus between an organism and its environment can shape the organism's growth and fitness through its biochemical demands for these elements and how this may provide a framework for linking ecosystem ecology and evolutionary biology. The contribution by F. Stuart Chapin III and colleagues mixes community and ecosystem ecology with social sciences to propound a new framework for understanding and predicting the future dynamics of human-dominated biological systems and how we might better manage and ameliorate human impacts. My contribution with R. Stoks uses molecular systematics, functional phenotypic studies, and conclusions drawn from field experiments of species interactions to reconstruct the evolutionary trajectories of two damselfly genera as they adapted and diversified into four distinct ecological habitats over the past 10–15 million years. Finally, S. D. Mitchell and M. R. Dietrich explore the philosophical tensions between unification and pluralism in the development of scientific understanding and illustrate their thesis with examples drawn from ecology and evolutionary biology.

These articles illustrate that much greater insights are developed by integrating research programs across disciplinary boundaries than by the piecemeal contributions of each discipline to a particular issue. By fostering the types of conceptual and empirical unifications that are exemplified by these articles, the American Society of Naturalists occupies a special place among international scientific societies.

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