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Some directions in ecological theory

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Abstract. The role of theory within ecology has changed dramatically in recent decades. Once primarily a source of qualitative conceptual framing, ecological theories and models are now often used to develop quantitative explanations of empirical patterns and to project future dynamics of specific ecological systems. In this essay, I recount my own experience of this transformation, in which accelerating computing power and the widespread incorporation of stochastic processes into ecological theory combined to create some novel integration of mathematical and statistical models. This stronger integration drives theory towards incorporating more biological realism, and I explore ways in which we can grapple with that realism to generate new general theoretical insights. This enhanced realism, in turn, may lead to frameworks for projecting ecological responses to anthropogenic change, which is, arguably, the central challenge for 21st-century ecology. In an era of big data and synthesis, ecologists are increasingly seeking to infer causality from observational data; but conventional biometry provides few tools for this project. This is a realm where theorists can and should play an important role, and I close by pointing towards some analytical and philosophical approaches developed in our sister discipline of economics that address this very problem. While I make no grand prognostications about the likely discoveries of ecological theory over the coming century, you will find in this essay a scattering of more or less far-fetched ideas that I, at least, think are interesting and (possibly) fruitful directions for our field.

Key words: *biomass overcompensation; causality; Centennial Paper; conservation biology; eco-evolutionary dynamics; ecological theory; NCEAS; quantitative ecology.*

INTRODUCTION

At the most essential level, the science of ecology seeks to understand the processes that determine the distribution and abundance of organisms, along with those that determine how organisms modify the abiotic environment. In an era of increasing anthropogenic impacts, ecologists also seek to predict how these processes will play out in a changing environment. What is the role of theory in these projects, and what theoretical advances might transform the science of ecology in coming decades?

Ecological theory is as varied as ecology itself, and is too vast to encompass in an essay such as this one. If you seek a review of the current state of theoretical ecology, I can instead point you to two (much longer) recent publications. The *Encyclopedia of Theoretical Ecology* (Hastings and Gross 2012) provides a survey of

the field in great breadth and satisfactory depth. It comprises heterogeneous articles on concepts (e.g., ecosystem services), analytical toolkits (e.g., branching processes), models (e.g., the Ricker model), and theories (e.g., the metabolic theory of ecology). One might reasonably expect a theoretical ecologist to be familiar with everything that is in this volume, but, lacking an integrative framework, it can be difficult to see the forest for the theoretical trees.

In contrast, *The Theory of Ecology* (Scheiner and Willig 2011a) focuses on the emergent properties of the theoretical forest, seeking integration and unification both within major subfields and across ecology as a whole. The philosophical premise is that a theory can be expressed as a collection of general principles or propositions that can be linked to specific models (Scheiner and Willig 2011b). Some of the proposition lists in the volume are useful and compelling: for example, the six propositions of “the theory of niches” (Chase 2011) provide a comprehensive high-level overview of coexistence theory. Some of the other proposition lists, I find, do not capture the essence of the theory being described, but most of the chapters provide valuable syntheses of the models and sub-theories within their domains.

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I should probably pause here and say something about what I think scientific theory is and does. I am no philosopher of science, but in practice I view theory as being a collection of supportable statements about how a system works and how these processes lead to patterns that we might, in principle, observe. The statements need to be precise and unambiguous, and based on rigorous reasoning. In practice, this means that that expression and demonstration of theory usually needs to be mathematical, for verbal statements tend to be linguistically ambiguous, and verbal reasoning can be easily led astray by the mental heuristics and imperfect analogies that we use to make sense of the everyday world (rigorous verbal analysis *is* possible, but it tends to be voluminous). A theory may be very general, or it may be tailored to a specific empirical system; we tend to call the latter “models,” but I think of all theory as being a model of reality. There is an important role for verbal and graphical statements of theory: to communicate the essence of the theoretical insights to those who are not fully fluent in the requisite mathematics. Indeed, this communication is essential if theory is to substantially influence the field; but such statements are generally not a robust starting point for extending and elaborating theory, or exploring its implications.

Two innovations have transformed ecological theory in recent decades, without which the ideas I want to discuss in this essay would not be possible. The first is the introduction of stochastic processes into our theory and models. At a broad conceptual level, stochasticity leads to outcomes that are impossible with simple deterministic processes alone, and has transformed areas such as population dynamics and coexistence theory; at a more tactical level, incorporating stochasticity explicitly into models opens new doors for linking theory to data. The second innovation is the development of fast computers. This has allowed us to analyze nonlinear and stochastic models that were previously intractable, and has greatly increased the richness and detail of ecological theory.

In the rest of this essay, I will discuss three themes around the changing role of theory in ecology. The first involves the link between theory and data that I alluded to in the previous paragraph, and a personal story about the transformation in the relationship between the two. Second, I explore the strategic addition of realism to ecological models, which can reveal general insights that would be difficult to uncover by tinkering directly with simple models. Finally, I turn to the challenge of a changing planet, and consider how theory can help us predict the future in ways that usefully inform management decision-making.

THEORY AND EMPIRICISM

As a graduate student in the early 1990s, I saw what looked like a vast divide between “theoretical” ecology, which was published in journals like *Theoretical Population Biology* and was 100% math, and “real” ecology, which was published in journals like *Ecology*

and used experimental data and statistical hypothesis tests to address narrowly proscribed empirical questions. I was taught that models, which abstracted away so much of biological complexity, could not hope to fit or predict actual data, and instead provided (at best) qualitative insights into pattern and process. Unfortunately, relatively few of us on the theory side were adept at translating these insights into forms that empiricists could incorporate into their research. Furthermore, there was a general sense, at least among dynamical systems folks like me, that long-term data collection was needed to test even these qualitative insights, and that such data (aside from some overworked collections such as fur-trapping records) did not (and probably could not, given the three-year grant cycle) exist.

Thus the inaugural working group at the National Center for Ecological Analysis and Synthesis (NCEAS), which I joined as a postdoc, seemed extraordinary: bring together theorists, statisticians, and empiricists to go beyond the usual theoretical conclusion (“these n ecological processes can all generate population cycles”) and the usual empirical conclusion (“this population is cycling”) to ask “*which* of the n cycle-generating processes is causing cycles in *this* population?” There was analysis: deepening our understanding of stochastic dynamical systems, customizing canonical mechanistic models to match the particularities of the populations, developing and testing statistical tools to quantitatively assess how well the mechanistic model predictions match the time series in oscillating systems. There was synthesis: we incorporated all kinds of additional empirical information about the population besides the time series itself, and forced the models to be consistent with them (e.g., “can host–parasitoid models create cycles without requiring the peak parasitism rate to be substantially higher than has ever been observed?”). It was often frustrating, and a huge amount of fun.

In retrospect, it is clear that some of this cross-fertilization and integration of statistical and mechanistic models had been occurring already, outside the confines of my graduate department. For example, Ray Hilborn and Marc Mangel (1997) were writing *The Ecological Detective*, which soon became a mainstay of graduate reading groups, popularizing the use of likelihood-based techniques to fit simple process-based ecological models to data. Furthermore, many of these techniques had long been used in fisheries science and biological control, which have the explicit mission of predicting the dynamics of particular empirical systems. An independent line of research used autoregressive models to unify the statistical description of time series data with mechanistic models of population dynamics (e.g., Stenseth et al. 1996). Furthermore, many ecologists pursued both theoretical and empirical work, although often the two were linked only at a broad conceptual level. Nevertheless, two lines of evidence illustrate the novelty of the integrative approach pursued by our working group. First, I was able to obtain the postdoc

with a fairly transparent bluff about my statistical abilities: very few students were being trained in both theory and statistics. Second, once we got beyond proofs of concept (Kendall et al. 1999) and were drawing ecological conclusions about ecological processes in particular populations (Turchin et al. 2003, Kendall et al. 2005), editors and reviewers wanted us to reframe the papers as being about methods—“here’s a mathematically complex method, and here’s an illustrative example of how it could be applied to real data (but we don’t really care about, or even believe, the ecological implications).” The approach, so far from the empirical convention of controlled experiment/hypothesis testing/ANOVA table, was simply not viewed as a credible way of drawing empirical conclusions—even by the theoretical ecologists who were reviewing the papers!

Our working group turned out to be the harbinger of the “new normal” at NCEAS, driven mostly by the incredibly talented young ecologists who worked there as postdocs. Those who, like me, had been trained in mathematical theory and modeling, were entranced by the growing collection of spatially, temporally, and taxonomically extensive data sets being assembled by the working groups (as well as the impressive Global Population Dynamics Database assembled at the Centre for Population Biology; NERC Centre for Population Biology 1999). Those with a background in empirical and statistical analysis were won over by the ability of models to make sharp, quantitative predictions. Facilitated by the growing power of computers, which allowed interactive analyses of nonlinear stochastic models, a new type of scientist emerged, at NCEAS and elsewhere: the integrated statistical and mechanistic ecological modeler.

First popularized by Hilborn and Mangel (1997), the key tool of this new generation of quantitative ecologists is the data-constrained dynamic model, which provides a framework by which conceptual understanding of ecological processes can be translated into concrete predictions of particular outcomes. There are two main ways to generate these data constraints. First, some model parameters can be measured directly. For example, matrix population models and their relatives (Easterling et al. 2000, Caswell 2001) and analogous individual-based models (e.g., Vortex; Lacy 1993) are built up from short-term processes of birth, growth and survival, which are sometimes easily observable in the field; such models allow ecologists and conservation biologists to translate short-term observations into long-term projections. In contrast, inverse procedures estimate parameters (and even model structure) by trying to get the model to generate spatial and temporal patterns that match the observations (Wood 1997). Advances in computing power and software usability are important here; but so is the close connection between the models and empirically measurable quantities. The use of Bayesian approaches (such as Markov chain Monte Carlo as implemented in BUGS; Link et al. 2002, Kéry

2010) to link a greater variety of data sources to dynamic models, as exemplified by integrated population models (which can combine direct estimation of some parameters with inverse estimation of others; Besbeas et al. 2002, Abadi et al. 2010) are likely to further enhance the utility of theoretical models for practical ecological application; and continues to blur the distinction between “theory” and “statistics.” For example, when multi-state mark-recapture models are used to estimate parameters of stage-structured population models (e.g., Fujiwara and Caswell 2001), the statistical and mathematical models have exactly the same structure, allowing accurate propagation of correlated uncertainty in the parameter estimates. Increasing numbers of empirical studies are being designed, not around classical, statistical, hypothesis testing, but instead using models that have emerged from the theoretical realm, to examine the magnitudes of, and relative importance of, multiple interacting factors on biological processes and outcomes (e.g., Johansson et al. 2012).

Training the next generation

A prominent theoretical ecologist once remarked to me that NCEAS proposals had too much synthesis (bringing together diverse data sets) and not enough analysis (deepening understanding through the application and development of advanced quantitative techniques). How can we ensure that quantitative ecologists have the methodological depth they really need? Such depth is hard, because the relevant domain of knowledge is broad: a deep mathematical understanding of dynamical systems and stochastic processes; thorough fluency in, and awareness of the limitations of, biometry, econometrics, and a vast array of “modern statistics”; the ability to write fast and numerically reliable code that is also transparent and reproducible; as well as all the ecological principles and theories that we would want any ecologist to know. We simply do not have a “canon” in these areas. However, the development of such a canon, looking both at high-level concepts like those in the *Encyclopedia of Theoretical Ecology* and at underlying mathematical fundamentals such as the Random Perron-Frobenius Theorem (Ruelle 1979), would be a valuable project of the Theoretical Ecology Section of the ESA. Perhaps it is too much to expect of a graduate student to master all of this; but I have observed individuals who are self taught in one or more of these areas (including myself) being surprised by phenomena that are actually well understood (such as the emergence of chaotic transients in stochastic nonlinear dynamical systems). We each should develop sufficient familiarity with a broad enough range of principles and approaches (beyond our own area of deep expertise) that we know when to seek out a collaborator. The field of integrated statistical and mechanistic ecological modeling emerged organically, but now that we see its value, we should start to cultivate it more systematically.

INCREASING BIOLOGICAL GENERALITY FOR ECOLOGICAL THEORY

In an influential essay published nearly one-half century ago, Levins (1966) suggested that we cannot have all three of generality, realism, and precision in a “manageable” model, which leads naturally to three strategies. The first, sacrificing generality, is evidenced today in detailed models of particular systems which, at their best, expand our understanding of empirical patterns in ways that complement conventional statistical analysis, in particular through the ability to do controlled numerical experiments on the model in ways that are impossible for large ecological systems. The third, which Levins himself claims to prefer, sacrifices precision (i.e., quantitative predictions). This third strategy has generally gone into decline as ecology as a whole became more quantitative, although the recent development of “partially specified models,” in which parametric functional forms are replaced by splines (Wood 2001), sort of falls within this approach. The second, which is where I spend most of my time, is to sacrifice realism in favor of generality (models without too many biological details apply broadly) and precision (simple models are analytically tractable). In the areas I know best (population dynamics and few-species community models), we rely on very old foundations of this type: the logistic model and its discrete-time relatives, the Lotka-Volterra competition model, the Nicholson-Bailey host-parasitoid model, the Leslie age-structured population model, the Rosenzweig-MacArthur predator-prey model, and the Levins metapopulation model.

I increasingly believe that many of us who work in this tradition have given up too easily on the realism dimension, and that there are aspects of organismal biology that we can incorporate into our models, without adding too much conceptual complexity, that will generate new general ecological insights and will constrain the space of ecological dynamics in ways that treating organisms as simple physical particles does not. I’ll make this notion more concrete in a moment, but first I want to comment on the process of adding biological detail to simple models.

It is easy to forget that the simple models we learn from textbooks are not *idealizations*, but rather cartoon *approximations* from which most biology has been abstracted away. As a robust simplification of reality, they apply only if certain assumptions hold, such as being very close to equilibrium or resource dynamics being infinitely fast. It is tempting to increase the realism of models by encrusting additional detail onto the simple models that seem so paradigmatic. I’ll hold myself up as a role model: I investigated the population effects of differences among individuals by simply adding heterogeneity in birth or death rates into simple models, without thought for how the underlying biological differences might affect other aspects of the individuals’ life histories (Kendall et al. 2011, Stover et al. 2012). However, the nonlinearities inherent in biological

systems will often mean that adding a biological detail to an existing approximation will give different results from adding that detail to an underlying realistic model and repeating the approximation process. The latter is more likely to be a useful cartoon.

Explaining biomass overcompensation

Let’s look at an example where adding a little realism has generated a new class of general biological insights. Almost all organisms change in size throughout at least part of their development, as well as making qualitative changes in their biology (from non-reproductive juvenile to reproductive adult, for example). If resources are not limiting and environmental conditions are unchanging, one can formulate conceptually straightforward population models that incorporate empirically measureable size-dependent reproductive, death, and growth rates. But how should one incorporate “density dependence” into such a model? If the limitation is due to intra-specific competition for a shared resource, then it is likely that the declining resource level is likely to affect survival, growth, and reproduction of all individuals. One can justifiably argue that, at equilibrium, only one of those rates, impacting one of the life stages, will be limiting the population, and on this basis a density dependent function can be applied to one of the vital or growth rates, informed, perhaps, by empirical data on responses to varying density. But what if conditions change: the resource production rate goes up, or extrinsic mortality (from predation or harvest) goes up? It is not necessarily true that the same vital rate, or life stage, will remain the limiting factor on the population, so our modified simple model is an unreliable extrapolation tool.

What can we learn by making the implicit resource dependence explicit? This might lead us to develop a size-structured model of a consumer feeding on a resource, which has its own renewal dynamics; the feeding rate of an individual consumer depends both on its size and on the resource abundance. A dynamic energy budget model (Kooijman 2010) might provide the link between resource consumption and the individual’s growth, death by starvation, or reproduction; maturation into a reproductive adult might take place at a fixed size. A model of this sort, adding explicit resource dynamics to the model of Kooijman and Metz (1984), was described and analyzed by de Roos and Persson (2013:100–107). It has a seemingly curious property: over a range of resource densities, increasing the extrinsic mortality of the consumer (e.g., due to predation or harvest) leads to an *increase* in equilibrium juvenile or adult consumer biomass. This phenomenon, termed “biomass overcompensation” by de Roos et al. (2007), turns out to be common property of models with this general structure (de Roos and Persson 2013). Indeed, with sufficient care, and some restrictive assumptions, the fully size-structured model (which, being a system of partial differential equations, can be

tricky to analyze even numerically) can be approximated by a system of three ordinary differential equations (juvenile and adult consumers, and the resources). The assumptions include a particular allometry of size-dependent resource uptake and metabolism, and that the system be at equilibrium; the care includes specifying the maturation function such that rate at which juveniles become adults reflect the cumulative mortality over the (resource-dependent) time required to grow to maturity (de Roos et al. 2008b).

This simplified model also demonstrates the phenomenon of biomass overcompensation and it facilitates a conceptual understanding of the biological circumstances under which this result is likely to occur (for details, see de Roos and Persson 2013: chapter 3). In addition, this simplified model allows investigation of the effects of biomass overcompensation in multi-species communities. For example, it can create a form of Allee effect for a predator of the size-structured species: when the predator is at low density, the prey biomass is insufficient for the predator to persist, but with high predator density the biomass overcompensation in the prey (caused by the predator-induced mortality) allows the predator to persist (the bistability this creates has been suggested as a cause for the collapse of fisheries stocks; de Roos and Persson 2002). Likewise, two predators that feed on different stages of a size-structured prey can facilitate each other, as the predation on one stage creates biomass overcompensation in the other (de Roos et al. 2008a). This result greatly expands the range of ecological circumstances under which we might see facilitation (typically thought to be primarily the domain of mutualistic interactions).

This new cartoon, which retains key dynamical properties without the burden of explicitly modeling the underlying mechanism, could not have been found by just adding detail to existing simple models. Rather than adding phenomenological density dependence to a size-structured model, resource dependence was made explicit and dynamic. This step was not in itself revolutionary: the fact that dynamic resources can qualitatively change system dynamics, while often ignored, has long been known (e.g., Armstrong and McGehee 1980). Indeed, the structural form of the consumer–resource model derived by de Roos et al. (2008b) had already been developed and studied (Yodzis and Innes 1992). However, the particular form of the maturation function, which is key to making the stage-structured model a valid approximation of the size-structured model, and hence reproducing the phenomenon of biomass overcompensation, would not have been found without building the more mechanistically realistic model and then analyzing its properties at equilibrium.

Now, the purpose of the preceding paragraphs is not to demonstrate that I'm a fan of de Roos and Persson's work (although I certainly am), but to illustrate that adding a bit more biological realism to our general and precise models can illuminate new realms of ecological

understanding. Admittedly, the size-structured models *look* complex, requiring a page or more of equations to fully explain, but the model is conceptually straightforward. To the uninitiated, this complexity may falsely give the impression that the model has so many parameters that a comprehensive analysis would be impossible. Indeed, as a graduate student, I wrote a scathing review (fortunately only seen by my committee members) to this effect. However, as this biological complexity is based on physiological processes, the parameters are strongly constrained even when looking across a wide range of taxa (de Roos and Persson 2013), so that, despite the biological richness, there are only a relative handful of parameters that need to be explored in an analysis of the model. Many avenues in which to explore the consequences of biomass overcompensation still remain; more importantly, in many other domains of theoretical ecology the addition of modestly more biological realism is opening the way to ecological discovery.

Trade-offs, constraints, and eco-evolutionary dynamics

One such area is the field of eco-evolutionary dynamics. It has become clear that populations can exhibit evolutionary change on ecological timescales, and that these evolutionary changes can affect ecological dynamics in surprising ways (Pelletier et al. 2009). This was the topic of an Ignite session at the 2013 ESA annual meeting, and presents an important challenge to ecological theory, which still typically assumes that parameters are fixed or fluctuate stochastically. The distinguishing feature of eco-evolutionary dynamics is the feedback between evolution and ecology (Post and Palkovacs 2009).

The key element of such models is a trade-off, such that selection on one trait or in one context (such as resistance to predation) leads to declining performance in another (such as reproduction). Trade-offs may be empirically observed (e.g., Miller et al. 2012), although they can be obscured by heterogeneity in individual quality (which creates positive correlations between life-history components; Hamel et al. 2009); life-history theory often simply assumes the existence of trade-offs between components of fitness (Roff 1992). However, eco-evolutionary theory currently does not encompass generalizable trade-off mechanisms. Models of specific systems use trade-offs that have been empirically observed in those systems (e.g., Jones et al. 2009), whereas more general models simply assert a trade-off between quantities such as survival and reproduction. The former are not generalizable, and the latter, while based on broad biological insights, are not mechanistic (quantities such as survival rate or population growth rate are not fundamental traits, but rather the *outcome* of (typically multiple) phenotypic traits interacting with the individual's state and the environment).

Evolutionary studies of trade-offs have different shortcomings. Their focus is on the genetic basis for

correlations between traits, generated by processes that give rise to linkage disequilibrium or pleiotropy (Roff and Fairbairn 2007). Two common conceptual models for the existence of negative trade-offs between traits that each positively influence fitness are that the traits are both functionally redundant and costly, or that the traits depend on a shared limiting resource (Agrawal et al. 2010). However, the ecological and physiological models employed in these studies are often unrealistic. For example, to explain the often observed pattern that correlations between traits that share a resource are positive, de Jong and van Noordwijk (1992) developed a model (commonly called the “Y model”) in which one gene controls the resource acquisition rate and another controls the allocation between the traits of interest; large variation in the former can swamp the negative trade-off between the traits that would be expected if resources were fixed. However, this model does not take into account the bioenergetics and ontogeny of resource acquisition and allocation, simply assuming that the resource acquisition ability is a fixed trait and that the traits of interest respond linearly to the total resources allocated to them.

This presents an opportunity to add usefully general realism by explicitly incorporating ecologically derived energy allocation models, such as dynamic energy budget models (Kooijman 2010). These include considerably more ecological realism than the evolutionary Y models, and allow explicit links to fluctuations in resource supply and conditions. In this case, the relevant trait is the (potentially state-dependent) allocation rule, such that, for example, selection for early reproduction will change the allocation rule in a way that may slow growth and/or make the organism more vulnerable to starvation. Incorporating biologically realistic constraints and within-individual processes into eco-evolutionary models should move us towards a more general understanding of when evolutionary changes are likely to affect ecological dynamics, as well as helping us understand coevolutionary fitness landscapes when interacting species act on very different time scales (e.g., Gilchrist and Sasaki 2002).

THEORY IN SERVICE TO NATURE AND HUMANS

The psychologist Martin Seligman, writing in defense of applied psychology, suggests that strong basic science can only emerge on the foundations of applied work, pointing to engineering and the predictions of eclipses as the antecedents of physics, and gunpowder and the alchemical search to create gold as the antecedents of chemistry (Seligman 2011:59–61). Many of the enduring elements of ecological theory also have applied roots: for example, branching process models (now used to understand demographic stochasticity and genetic drift) were developed to answer Francis Galton’s questions regarding the persistence of family names (a very applied question if one is living in a 19th-century patrilineal aristocracy; Allen 2012). Similarly, Vito Volterra devel-

oped his predator–prey model in response to practical questions about fisheries management (Volterra 1926, Kingsland 1995:106–107). In the third quarter of the 20th century, the science of ecology (at least as represented by the ESA) moved away from these roots, increasingly engaging in what Seligman would call “puzzle-solving” than in problem-solving. By the 1980s, however, it had become clear that humans were influencing ecological processes everywhere on the globe, and ecologists are now called to solve practical questions not just around biodiversity conservation, but also around fundamental sources of human welfare such as the provision of ecosystem services and adaptation to climate change.

Theory played a tremendous role in the early history of conservation biology. For example, notions of how rarity relates to endangerment, now fully codified in the IUCN Red List, have their roots in a series of highly mathematical papers, ultimately synthesized by Lande (1993), relating extinction risk to carrying capacity, growth rate, and various sources of stochasticity. The design principles used by systematic conservation planning draw on ecological theories such as those of island biogeography and metapopulation dynamics (Margules and Pressey 2000). Demographic theory and models, once theoretical abstractions, are now applied routinely in tools such as population viability analysis (e.g., Akçakaya et al. 2004), which attempt to project the fates of particular species under various scenarios. However, we are finding that there are limits to the quantitative application of such models in the face of parameter uncertainty and inherent stochasticity. Even a model that is right “on average” may not make useful predictions for a particular place and time (Ellner et al. 2002), and there may be irreducible limits to predictability in many ecological systems (Melbourne and Hastings 2009). There is also a need for further theoretical development; for example, the theoretical roots of conservation biogeography remain unintegrated (Whittaker et al. 2005), and the mathematical richness of modern conservation planning derives more from optimization and control theory than from explicitly ecological theory (Moilanen et al. 2009). How might we uncover new theoretical generalizations that can provide conceptual guidance to applied ecology?

One approach could be to explicitly consider evolution. Might a species subject to anthropogenic threat be able to evolutionarily or plastically adapt? Such “evolutionary rescue” is possible (Bell 2013), especially if the population size is large or the anthropogenic change is gradual (as in climate change; Hoffmann and Sgrò 2011). However, species that are rare or declining have little opportunity to express this response (e.g., Gomulkiewicz and Houle 2009), and an important challenge moving forward is to unpack the existing theoretical principles, along with emerging theory about the effects of community interactions on evolutionary rescue, in a form that can be applied to assess individual species of concern.

Identifying such species that are likely to survive is but one component of a triage approach to conservation (Bottrill et al. 2008). An equally important question is, “Which species are most likely to respond to intervention?” Demographic theory allows us to identify, from a sufficiently well-quantified life history, the life stages and vital rates where reducing threats will best improve that species’ prospects (e.g., Crouse et al. 1987). I’d like to propose that knowing something about a species’ evolutionary history may also provide guidance, even in the absence of intensive demographic study. For example, Lande’s (1993) synthesis of the dependence of extinction time on carrying capacity suggests that any species that is naturally rare (i.e., has persisted for a long time with a low carrying capacity) is likely to have a life history that exhibits rapid population growth at low density, low sensitivity to various sources of environmental stochasticity, or both—species without such characteristics would likely have gone extinct long before humans began to affect it. Such species would be expected to recover quickly if the anthropogenic factors that hold them below their natural carrying capacity can be removed. The rapid recovery of some island species, such as the Lord Howe Island Woodhen (Miller and Mullette 1985, Brook et al. 1997) and the Channel Islands fox (Coonan et al. 2010), is highly suggestive in this regard. Of course, we need to update Lande’s results (which are based on a simple unstructured model) to incorporate life history information and extinction-colonization dynamics, take into account the many ways to be rare (Rabinowitz 1981), focus on the anthropogenic impacts that are in fact reversible, and move beyond anecdotal examples. This seems to me to be an area ripe for impactful theoretical study.

DATA AND CAUSALITY

I want to close by returning to the interface between statistical and mechanistic modeling, and particularly to the data engagement part of that. Much of the data being used in such studies are observational, rather than experimental, and this will only increase as ecology enters the “big data” era. Drawing inferences about causality and mechanism from observational data is tricky. In fact, ecologists are often taught that it is actually impossible; “correlation does not imply causation” and all that. While explicitly incorporating theoretical models into the data analysis can help, it will still not rule out, in general, the possibility that the observed variables may covary because both are correlated with a confounding variable, or that the relationship between the variables of interest is obscured or distorted by the effects of an unobserved causal variable. Are we doomed to choose between cloaking our results in uncertainty and confidently hoping for the best?

The field of economics has some answers. There is a long history of association between ecology and economics: strong analogies between fitness and profit have allowed conceptual and theoretical tools to apply

in both fields; and bioeconomic models of natural resources and ecosystem services are central to much applied ecology. But economics also has an empirical side; and almost all of the data available to economists are observational. Thus econometrics, which looks superficially similar to biometry (both have a strong focus on linear models, although econometrics privileges regression rather than ANOVA), includes a diverse toolbox for rigorously drawing inferences from such data (notably, but not exclusively, the method of instrumental variables; Hanley et al. 2008, Kendall 2015). To be sure, these methods require finesse, and each requires certain data conditions that don’t always apply (I recommend collaborating with an economist to be sure to get it right; Armsworth et al. 2009); they also come with a cost of reduced statistical power. The economists I know also start from sound conceptual and/or mathematical theory before doing data analysis, and devote considerable effort towards thinking of, and analyzing, all the reasons that the patterns in their data might have other causes (much as was advocated over a century ago as the “method of multiple working hypotheses”; Chamberlin 1890).

If integrated statistical and mechanistic and statistical modelers can extend their existing toolboxes to emulate economists’ skepticism and attention to detail in the evaluation of causality, then we should be able to generate much more robust tests of ecological theory using large-scale observational data sets. The careful, model-driven analysis of such data will allow us to identify areas where adding biological realism to our theory and models can generate broad insights; I have suggested a few examples from my own areas of expertise, but I am sure there are many more. Both integrating theory with data and developing new theory may require us to rethink the way we train our students and ourselves. The payoff for this work will be a more complete understanding of the interplay between general principles, biological constraints, and ecological contingency. From this, we can use theory to make useful predictions (including bounding the uncertainty of the predictions) for the specific communities, ecosystems, and populations that sustain humans and their environments.

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