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# Advancing Ecosystem Science by Promoting Greater Use of Theory and Multiple Research Approaches in Graduate Education

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## Abstract

Since the inaugural edition of Ecosystems was published in 1998, ecosystem science has undergone substantial changes including the development of new research methods and an increasing emphasis on collaborations across traditional academic boundaries. In response to this transformation, we reflect on the current state of theory in ecosystem science, and make recommendations for training the next generation of Ph.D.-level ecosystem scientists. Specifically, we call for increased integration of theory into ecosystem science and outline the utility of iterating between theory and data generated by observations, experiments, and quantitative models. We recommend exposing graduate students to these three major approaches for generating data and propose strategies that students, advisors, and

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departments can employ to ensure this exposure. Ultimately, a successful training program will provide students with an understanding of key theories related to ecosystem science and how they interact with data, an appreciation for the interconnectedness of approaches to scientific inference, and a welldeveloped skill set in at least one approach—thereby empowering them to confidently tackle our pressing environmental problems. Although this is a daunting list of goals, continuing to advance our understanding of how ecosystems function necessitates a rigorous and well-developed training program.

**Key words:** training; inference; pedagogy; models; observations; experiments.

"Theory without data is sterile, while data without theory is uninterpretable." Levin (1989), page 244.

"The progress of ecosystem science is limited simultaneously by both theory and methods."

Sala and others (2000), page 1.

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In the proceedings of the 7th Cary Institute of Ecosystem Studies Conference (Pace and Groffman 1998), Steve Carpenter argued that multiple lines of inference are necessary to understand how ecosystems function, drawing on the metaphor of a four-legged table composed of theory, observations in space, observations in time, and experiments (Carpenter 1998, Figure 1A). We agree with this overall premise, but would like to elevate the importance of theory using an alternative metaphor (Figure 1B), in which theory is the basis for ecosystem science (as shown by the "floor"), interacting with a three-legged stool in which theory is tested using data generated by experiments, observations, and quantitative modeling (see Box 1 for definitions), and then modified as needed in response to data in an iterative process. Given this metaphor, we propose that (1) couching research in a theoretical context accelerates the efficiency and advancement of ecosystem science; (2) experiments, observations, and quantitative models provide complementary tests of theory that can inform applied solutions; (3) graduate students should be exposed to theory and to each of these approaches during their training even if they anticipate focusing on a particular approach; and (4) opportunities abound to better integrate theory and multiple approaches for collecting data into graduate training, at individual to institutional levels. Below, we explain our thinking on these issues.

## THE CURRENT ROLE OF THEORY IN ECOSYSTEM SCIENCE

Theory provides a critical framework for organizing fundamental scientific assumptions, uniting seemingly disconnected concepts with underlying principles, comparing empirical data to mathematical expectations, and generalizing findings from disparate study systems (Marquet and others 2014) and across spatial and temporal scales (Carpenter 1998). However, one of our Dartmouth colleagues likes to spark discussion by charging that ecosystem ecologists fail to engage theory. A cursory analysis using Web of Science suggests that there may be some validity to this claim. We calculated the annual percentage of papers containing the topic 'theor\*' in all papers published in the journals *Ecosystems, Ecology,* and *The American Naturalist* from 1998 to 2015 (Figure S1). On average, Ecosystems included a lower percentage of theory-based papers (7%) than Ecology (17%) or The American Naturalist



**Figure 1.** Metaphors for how ecosystem science should operate. **A** Carpenter's (1998) "table". **B** Our proposed alternative, which makes theory the foundation upon which to place data collection that relies on the interplay of experiments, quantitative models, and observations. Failure to include a strong theoretical foundation, or to balance different approaches to data collection, may lead to falling off the stool. In addition, the floor itself (that is, theory) is shaped by the combined activity and resulting findings from experiments, models, and observations.

(27%), and since its first publication year, the percentage of papers with the topic theor\* in *Ecosystems* has declined, whereas it has increased slightly over the same time frame in both *Ecology* and *Am Nat* (Figure S1). This analysis surely overlooks papers that engage theory without explicitly stating the term and fails to characterize the extent of engagement with theory (Scheiner 2013). At face value, however, it suggests that papers in *Ecosystems* engage with theory both less often and increasingly less frequently than two other leading ecological journals.

## TOWARDS A GREATER INTEGRATION OF THEORY AND DATA IN ECOSYSTEM SCIENCE

Buoyed by the contributions of theory to other areas of ecology (Kendall 2015), we encourage ecosystem scientists to put theory to greater use in informing project development and data collection. The most pragmatic way to approach a particular problem in ecosystem science (or indeed, any **Box 1.** Working definitions used in this paper for theory, models, observations, and experiments

A **theory** is a series of postulates, described either verbally or mathematically, which leads to a range of logical predictions and emergent generalizations given a limited set of assumptions. The postulates may or may not be true, and need to be tested using observations, experiments, and quantitative models (see Online Supplemental Material, Appendix 1).

A **model** is a simplification of nature. **Conceptual models** provide a simple, box and arrow type of sketch of how a researcher thinks the world might work, while **quantitative models** translate a conceptual model and its assumptions into mathematical equations that are then solved analytically or investigated using simulations. Here, we class conceptual models alongside theory, similar to Weathers and others (2013), and regard quantitative models as representations of a particular system, compared with the broader class of "theory," which applies more broadly (Shugart 2000).

**Observation** is measurement without manipulation to capture the system in its 'natural' state. Typically, this is seen as an attempt to describe patterns in nature, and to draw inferences about the potential drivers of those patterns. Observations have the advantage of being made at the spatial and temporal scales of inquiry, but the inferences drawn from observational studies are correlative, rather than causal, because of the inability to rule out other potential drivers of the observed pattern (that is, 'lurking' variables). In ecosystem science, observations include both 'snapshot' sampling of numerous ecosystems at one time and long-term studies within one or a few systems (Carpenter 1998).

An **experiment** involves a deliberate manipulation of the study system to test a hypothesis about the causal mechanism(s) that underlie a particular pattern, by comparison of manipulated vs. 'control' conditions. Experiments are the gold standard for determining causal relationships, but are sometimes conducted at such small spatial scales and over short temporal scales that they may not capture natural responses over the long term. However, recent innovations to deal with some of these limitations using distributed experiments that replicate the same small-scale design at numerous sites may help to resolve some of these concerns; examples include NutNet (Stokstad 2011) and LINX (LINX Collaborators 2014). Whole-ecosystem experiments also play an important role in ecosystem science (Carpenter 1998).

A core premise of this paper is that most questions in ecosystem science will be best answered by employing a combination of approaches, which regularly engages with the underlying theoretical framework, draws on the unique contributions of each approach, and provides ample opportunity for interplay among approaches.

science) is to start with an understanding of how relevant theories relate to the specific problem at hand, in order to develop a framework for understanding that can be brought to bear on a particular problem. For example, if a new graduate student is interested in investigating the biogeochemical response of northeastern forests to climate warming, there is no need to "start from scratch." A wealth of theories already provides a valuable perspective to guide the start of this inquiry (Suppl. Material, Appendix 2), including the metabolic theory of ecology (Brown and others 2004), biological stoichiometry (Sterner and Elser 2002), biodiversity-ecosystem function (Loreau and others 2001), and plant-soil feedbacks (van der Putten and others 2013).

Integration of theory and data provides many benefits. First, it enables the research to become an immediate part of an existing structure of knowledge and minimizes the risk of missing relevant work that can inform best approaches to addressing a particular question. These benefits can accelerate scientific progress, which is increasingly important giving funding constraints. Moreover, beyond providing qualitative background information, theories with some overlapping assumptions or postulates may provide alternative pathways to explaining similar phenomena (Chamberlin 1965). Good theory also explicitly identifies the independent and dependent variables necessary to verify assumptions and test predictions and leads the researcher toward appropriate methodological approaches, which may include experiments, observations (across space and through time), and quantitative models. Thus, framing ecosystem science questions in the context of relevant theories streamlines research planning and maximizes limited resources. Moreover, theory provides a common language through which scientists with different methodological skill sets (for example, modelers vs. empiricists) can communicate.

Once data are collected, the challenging process commences of determining how resulting information supports or challenges the motivating theory. Theories are approximations of some true underlying process and therefore are in continual need of refinement (Marquet and others 2014). Integrating data and theory may be as simple as qualitatively confirming that, under the original set of assumptions, predictions from theory hold in a new study system. Alternatively, data may lead to increasing generality of a theory by requiring mathematical tweaks to theoretical postulates or revision, addition, or rejection of the underlying assumptions. Exciting advancements in science often occur when data don't fit theoretical predictions despite adhering to underlying assumptions

Level	Strategy	Additional student benefit(s)			
Individual student	Search for programs that emphasize theory and value diversity in research approaches	Self discovery			
	Read broadly across different bodies of literature Conduct a systematic review or meta-analysis	Interdisciplinary literacy Interdisciplinary literacy			
	Mentor undergraduate researchers	Technical proficiency Teaching Confidence building Leadershin			
	Talk about science informally in a variety of settings (for example, over coffee, beer, ice cream)	Conversational flexibility			
	Recruit thesis committee members who can of- fer a diverse set of tools and approaches	Confidence building Negotiating Networking			
	Engage in local education and outreach activi- ties with the public	Science communication Conversational flexibility Teaching Leadership			
	Meet with scientists in non-academic settings: government agencies, non-governmental organizations, etc.	Science communication Conversational flexibility Networking			
Student-advisor interactions	Challenge students to develop breadth	Interdisciplinary literacy Confidence building Self discovery			
	Encourage students to take courses that broaden their skill sets	Interdisciplinary literacy Technical proficiency			
Lab group	Discuss papers that use different approaches	Critical evaluation Interdisciplinary literacy Teamwork			
	Write lab-wide papers that draw on individuals' complementary expertise	Collaborative writing Teamwork			
	Meet jointly with other lab groups who use different approaches or work on different ecosystems	Conversational flexibility Interdisciplinary literacy Networking Scientific collegiality			
Grad student peers	Help colleagues with their field work (and have them help you)	Technical proficiency Teamwork Confidence building Teaching			
	Develop coding/programming partnerships	Technical proficiency Teaching Teamwork			
	Organize and participate in short-term research derbies and longer-term working groups, journal clubs, and short courses	Teamwork Leadership Teaching Collaborative writing			

Table 1.	Strategies to Help	Graduate	Students	Become	Exposed to,	and	Comfortable	with,	Both	Theory	and
a Breadth	of Research Appro	oaches									

Level	Strategy	Additional student benefit(s)		
Programmatic	Require weekly program-wide research-in-progress	Scientific presentation		
	seminars	Critical evaluation		
		Scientific collegiality		
	Include outside expert on thesis committees	Networking		
		Scientific collegiality		
	Sponsor multi-disciplinary research colloquia	Critical evaluation		
	Pursue multi-disciplinary training grants (for exam-	Interdisciplinary literacy		
	ple, National Science Foundation Research	Science communication		
	Traineeship)	Technical proficiency		
		Teamwork		
		Teaching		
		Critical evaluation		
		Networking		
	Offer structured learning opportunities (for example,	Technical proficiency		
	term projects, short courses, rotations outside the primary lab, complementary teaching assis- tantships)	Teaching		

Table 1. continued

"Level" refers to the agent to whom the strategies are directed; "Additional student benefit(s)" refers to the potential positive outcomes from pursuing a particular strategy.

(Duarte and others 2003). In such cases, data may drive the development of a new competing theory.

Research projects in ecosystem science will vary in their extent of engagement with theory [for example, drawing on vs. developing vs. testing theory; sensu (Scheiner 2013)], depending on the question and empirical findings at hand, the scientists' area of expertise and skill sets, and the degree to which the study system meets the general assumptions of some theory. We don't expect every project to require the development of new theory; instead we suggest that drawing on theory to inform hypothesis development and data collection serves as the least common denominator in ecosystem research. In short, because incorporating theory provides benefits at the level of the individual researcher and the scientific field, it should underpin all research projects, regardless of the methodological approach employed.

## IMPROVING EXPOSURE TO THEORY, Observations, Experiments, and Quantitative Models

We believe that exposure to the major theories of ecosystem science (for example, Box S1) and to each of the major approaches for data collection (quantitative models, observations, and experiments) is an essential part of a well-rounded training program. Even if a particular student plans to rely primarily on

either modeling or empiricism, understanding the strengths and limitations of the other approach(es) will improve one's own project as well as one's ability to communicate more effectively within collaborative research teams. Because quantitative models are abstractions of reality, only as good as the input data and assumptions used to construct them (Duarte and others 2003), much can be learned from the mismatch between model predictions and empirical data. It is important for modelers to know how the empirical data used to develop and test models are obtained, to be able to assess the potential limitations of the data (and model) and to meaningfully interpret a predicted difference across different modeling scenarios. On the other hand, it is also important for empiricists to know how their data are (or might be) used by modelers, as well as what the limitations of models might be. Understanding how quantitative models are developed may allow empiricists to tweak and fine-tune data-collection protocols, thereby maximizing the likelihood of data being used in future models. For example, designing experiments to collect data on specific quantitative, rather than nominal, treatments can facilitate model development (Cottingham and others 2005).

Additional advantages of broad exposure to theory, quantitative models, observations, and experiments include developing a strong understanding of the flow of information between data (whether from observations, experiments, or quantitative models) and theory. Trying different approaches also offers early career researchers opportunities to determine what they like and what they are good at, which may inform both their dissertations and long-term career trajectories. Further, we hope that broad exposure promotes open-mindedness about the complementarity of different approaches, which may facilitate cross-talk among researchers with different specialties—an important skill-set for conducting the kinds of interdisciplinary, teambased projects typical of ecosystem science.

Importantly, we are not advocating top-down mandates whereby all graduate students need whole dissertation chapters devoted to each type of research approach, that is, dissertations with a chapter each on modeling, field observations, and mesocosm experiments. Rather, there are lessprescriptive ways to introduce trainees to different approaches and to build a strong skill set in at least one of these areas (Table 1). Moreover, exposure does not have to happen solely in graduate school; it can begin as an undergraduate, continue between degrees, and extend into postdoctoral research. In fact, intentional exposure may not even be needed, if program directors develop structures that deliberately nudge students toward experiencing multiple approaches and toward being opportunistic about unexpected opportunities (Table 1).

## **S**YNTHESIS

In conclusion, we suggest that aspiring ecosystem scientists learn the core theories of ecosystem science and use them in framing their research questions; get exposed to and become comfortable with experiments, observations, and quantitative models; build a strong skill set in at least one of those approaches; and be open to opportunities to learn new things when needed. Although many opportunities exist for advisors and programs to nudge graduate students toward integrating theory and multiple approaches into their training (Table 1), ultimately the onus is on individuals to develop the self-confidence to be fearless about crossing disciplinary boundaries to learn whatever new tools and approaches are needed to address a particular research question.

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#### REFERENCES

- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–89.
- Carpenter SR. 1998. The need for large-scale experiments to assess and predict the response of ecosystems to perturbation. In: Pace ML, Groffman PM, Eds. Successes, limitations, and frontiers in ecosystem science. New York: Springer. p 287–312.
- Chamberlin TC. 1965. The method of multiple working hypotheses. Science 148:754–9.
- Cottingham KL, Brown BL, Lennon JT. 2005. Knowing when to draw the line: the role of regression and ANOVA in ecological experiments. Front Ecol Environ 3:145–52.
- Duarte CM, Amthor JS, DeAngelis DL, Joyce LA, Maranger RJ, Pace ML, Pastor J, Running SW. 2003. The limits to models in ecology. In: Canham CD, Cole JJ, Lauenroth WK, Eds. Models in ecosystem Science. Princeton (NJ): Princeton University Press. p 437–57.
- Kendall BE. 2015. Some directions in ecological theory. Ecology 96:3117–25.
- Levin SA. 1989. Challenges in the development of a theory of community and ecosystem structure and function. In: Roughgarden J, May RM, Levin SA, Eds. Perspectives in ecological theory. Princeton (NJ): Princeton University Press. p 242–55.
- LINX Collaborators. 2014. The Lotic Intersite Nitrogen Experiments: an example of successful ecological research collaboration. Freshw Sci 33:700–10.
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–8.
- Marquet PA, Allen AP, Brown JH, Dunne JA, Enquist BJ, Gillooly JF, Gowaty PA, Green JL, Harte J, Hubbell SP, O'Dwyer J, Okie JG, Ostling A, Ritchie M, Storch D, West GB. 2014. On theory in ecology. Bioscience 64:701–10.
- Pace ML, Groffman PM. 1998. Successes, Limitations, and Frontiers in Ecosystem Science. New York: Springer.
- Sala OE, Jackson RB, Mooney HA, Howarth RW. 2000. Introduction. Methods in ecosystem science: progress, tradeoffs, and limitations. In: Sala OE, Jackson RB, Mooney HA, Howarth RW, Eds. Methods in ecosystem science. New York: Springer. p 1–3.

- Scheiner SM. 2013. The ecological literature, an idea-free distribution. Ecol Lett 16:1421–3.
- Shugart HH. 2000. Ecosystem modeling. In: Sala OE, Jackson RB, Mooney HA, Howarth RW, Eds. Methods in ecosystem science. New York (NY): Springer. p 373–88.
- Sterner RW, Elser JJ. 2002. Ecological Stochiometry: The Biology of Elements from Molecules to the Biosphere. Princeton University Press: Princeton (NJ).
- Stokstad E. 2011. Open-source ecology takes root across the world. Science 334:308–9.
- van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA. 2013. Plant-soil feedbacks: the past, the present and future challenges. J Ecol 101:265–76.
- Weathers KC, Strayer DL, Likens GE. 2013. Introduction to ecosystem science. In: Weathers KC, Strayer DL, Likens GE, Eds. Fundamentals of ecosystem science. Waltham (MA): Academic Press. p 3–23.