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Teaching with principles: toward more effective pedagogy in ecology

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Abstract. Ecology is a complex and dynamic field and, as communicators of our discipline, faculty should be able to define a set of core principles that underpin and create ecological pattern and process. The pedagogical value of defining and drawing on a concise set of disciplinary principles and concepts is well grounded in research on cognition. Here, we present a set of seven core ecological principles from a graduate-level course in ecology as an example of how a pedagogical approach based on principles can provide students with essential components of a mental model shared by their instructor and classmates, and from which a deeper understanding of ecological pattern and process can be achieved. We also provide a series of recommendations to stimulate faculty to think more deeply about the teaching and learning of ecology so that they can identify a set of concepts and principled reasoning appropriate for their teaching circumstance.

Key words: ecological concepts; ecological principles; ecology learning; ecology pedagogy; ecology teaching.

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INTRODUCTION

All science is either physics or stamp collecting.
—Ernest Rutherford (1962)

The quote above is subject to a number of interpretations, but the most common is that science should lead us to general and predictive theories, which will enable greater understanding of the natural world—what Rutherford claimed of physics. Otherwise, science will be little more than cataloging and organizing elements and attributes of the world we live in. Such an assertion has particular relevance for how ecology is taught to students and communicated to the public, especially in this era of unprecedented global environmental change. Given the enormous number of individual species responsible for ecological pattern and process, the spatial and temporal complexity of the physical environment within which these interactions occur, and the numbers and types of interactions possible, there is perhaps no discipline of science in which "stamp collecting" makes *less* sense than ecology. Indeed, such complexity demands that as educators and, more generally, communicators of our discipline, ecologists attempt to identify and define a set of core principles that foster greater understanding of the world in which we live.

WHY A SET OF CORE PRINCIPLES IS IMPORTANT FOR PEDAGOGY

The pedagogical value of defining and drawing on a concise set of disciplinary principles and concepts is well grounded in research on cognition and learning. Faculty, as expert ecologists, have flexible and evolving mental constructs that they use when faced with an ecological question or situation. In the classroom, the problem is that: (1) most faculty don't clearly articulate these constructs to their students, (2) they assume that students understand these ways of thinking or that they can adopt them easily, and (3) students may not have the same understanding of these ideas at all (Wilson et al. 2006). As an example, for ecologists the phrase "balance of nature" will likely evoke concepts of resilience, stability, and both equilibrium and non-equilibrium models (e.g., Pimm 1991). In contrast, less experienced ecology students may have ill-defined ideas about these concepts or an understanding strongly influenced by the popular use of this phrase (e.g., that even with major disturbances such as climate change, the earth will regain its innate balance). Thus, it is critical for instructors to clearly communicate to students the underlying models for their discipline. In this way, students with naïve conceptions of ecology can contrast their "understanding" with their professor's and build a more sophisticated comprehension of the field. This in turn requires faculty to formally articulate their mental models of ecology into a set of key principles and to keep returning to these ideas in different contexts throughout the class.

Research on expert vs. novice learners is directly applicable to the pedagogical approach we espouse here. Thirty years ago, foundational research by Chi et al. (1981) demonstrated that expertise develops more quickly when people have effective mental models to which they can "attach" specific ideas, facts and concepts. More recent studies have focused on students' abilities to understand ecological concepts, specifically on the nature of causality (e.g., Grotzer and Basca 2003). Here, linear cause-and-effect thinking, typical of younger and introductory level students, has been shown to contrast sharply with the ecology experts' understanding of domino (branching or radial), re-entrant (feedback loops and cyclic patterns) and mutual causality (reciprocal patterns). A related area of research concerning novice/expert understanding of "complex systems", characterized by interacting levels of organization, interconnections, and invisible processes, is clearly relevant to helping students gain a deeper understanding of ecology. For example, Jacobson (2001) found that undergraduates, as novices, discussed complex systems problems in the context of a centralized force or predictable action effects. In contrast, experts referred to emergent properties resulting from decentralized interactions and nonlinear, random effects.

Despite the demonstrated value of mental models and concepts, a fact-based approach to teaching is still too common today, despite claims to the contrary by faculty. Indeed, some studies have reported than almost 90% of questions asked of students on exams require only simple recall, not any conceptual understanding, and this approach has been linked to alarmingly low rates of student retention of content (Gardiner 1998). Ecologists have agreed that with respect to achieving broad ecological literacy, key concepts and principles must be taught, but of course this requires that we can agree on those concepts—a challenge currently not met by ecologists or even biologists in general (D'Avanzo 2008, Jordan et al. 2009). Indeed, Jordan et al. (2009) recently issued a call to ecologists to help address this need—not by producing laundry lists of concepts that we think constitutes ecology—but instead by focusing on a few key principles.

This paper presents one candidate set of core ecological principles that have been taught in a "Foundations of Ecology" class populated by nascent graduate students—students that are primarily in the research design phase of their academic programs. Primary goals of the course are to help students better understand and appreciate how ecology builds from and overlaps with other sciences, what makes ecology a unique and challenging discipline, and the core principles and concepts that underpin and create the patterns and processes we see in nature (sensu Lawton 1999). We present these principles from a pedagogical perspective, not with the goal of convincing others to adopt them. Instead, they stand as examples that have proven valuable in this "Foundations" course for providing students the essential components of a mental model that can be shared by their instructor and classmates, and from which a common understanding can be more readily achieved through class discussions, group assignments and readings.

We adopt a well-accepted definition of principles here as statements of the ultimate origin or cause of the essential elements or qualities of ecological systems. It is important to note that these principles are not attempts to explain away the often idiosyncratic nature of the results of ecological studies and the poor predictability of many of the generalizations in our field (Vepsalainen and Spence 2000, Lockwood 2007). Instead, we have adopted a non-equilibrium perspective (Wallington et al. 2005) and attempt to identify those fundamental principles of ecological systems, processes, and interactions that (1) lead to these very attributes and (2) provide overall limits to the behavior of ecological systems. It is critical to recognize, and emphasize to students, that many of these principles are not unique to ecology, but in total they are uniquely important for understanding ecological systems. Thus, we are answering the call of Jordan et al. (2009) by presenting a candidate set of principles that we believe have pedagogical value for both faculty and students.

Of course such an endeavor requires many caveats. First, we certainly do not claim that these are the fundamental principles to be taught in all ecology courses. Nor do we wish to debate whether there are general or universal laws in ecology, or suggest that the principles we present constitute an outline for a unifying theory of ecology (Lockwood 2007, Scheiner and Willig 2008). The literature is replete with discussion on whether or not fundamental laws, principles or unifying theories of ecology exist (see Dodds 2009 for a recent review). Indeed, there have been many attempts to identify these (Appendix). For example, Scheiner and Willig (2008) proposed a unifying theory for ecology that was based on seven fundamental principles. Following that, Dodds (2009) took a different approach and articulated 35 laws, five candidate laws, and nine "useful generalizations" for ecology. Although several of our principles differ, our approach focuses on a few broad principles and thus is more similar to that taken by Scheiner and Willig (2008).

Seven Pedagogical Principles of Ecology

Below, we present and provide very brief rationale for seven principles that together set broad limits to the complex and often unpredictable behavior of ecological systems. We offer these as one approach for articulating a set of foundational concepts that, when assimilated by students will lead to a deeper understanding of, and less confusion about, ecological pattern, process, and interaction. Some selected references are added to several of these to illustrate their relationships to both historical and foundational concepts in ecology, as well as their relevance today.

1. Ecological patterns and processes are underpinned by physical laws.—Ecological systems and interactions follow the laws of those scientific disciplines that provide the foundation of ecology as a discipline. Thus, fundamental laws of physics and chemistry ultimately constrain, not exclusively but in important ways, all ecological processes from the ecophysiological to global biogeochemical. For example, the thermal, physical, and chemical limits of the functioning of membranes and proteins provide the mechanisms that help determine process rates as well as potential boundaries for the distribution of life in general, and of individual species. Actual or realized process rates and boundaries are, of course, determined by many additional factors. Although the actual laws of physics or chemistry will likely not be (re-)taught to students as part of an ecology course, reminding them of these ultimate constraints as a foundation for their mental model is critically important. One way to do so is to cite examples of the consequences of a failure to recognize this principle. For example, early plant ecologists expected that plants growing at high elevation would have the ability to use carbon dioxide more efficiently than their low elevation counterparts because the partial pressure of carbon dioxide decreases significantly with altitude. They also hypothesized that low carbon dioxide at high altitude may ultimately limit the upward distribution of plants. Many studies were conducted to test this hypothesis and one high profile paper even reported evidence in support of this adaptation (Billings et al. 1961). Only later, was it realized that although partial pressures of carbon dioxide did indeed decrease with altitude, this was almost completely compensated by the increased rate of diffusion of carbon dioxide and other gasses at high altitude (Gale 1972) and thus there was no physical or biological basis to expect such adaptations in high elevation plants. In contrast, the power of this principle is evident in the development of metabolic scaling theory, which has as its basis, physical and chemical relationships between mass, temperature, and metabolic rates of organisms (Brown et al. 2004).

2. *Ecological systems are open but resources are finite*.—Ecological systems are energetically open, but one or more key resources are usually finite (or limiting), subject to consumption, and their transformations are constrained by thermodynamics (Principle 1). Open systems allow for an increase in order (or information) to accrue through time in ecological systems while not violating thermodynamic laws, and from a metapopulation perspective, openness may permit greater persistence and information flow (Kareiva 1990). Recognition that resources are finite, or the rate at which they become available is limiting, that resources are consumable, and that there are constraints on energy flow, provided the basis for well-known energetic and trophic concepts developed by Lindeman (1942). Further, such knowledge is essential for understanding most species interactions, and coupled with the abiotic limits in Principle 1, defines many of the axes of the niche—one of the most fundamental concepts in ecology (Hutchinson 1959, Leibold 1995). This principle is also key for understanding what limits maximum rates of population growth and energetic aspects of population regulation. Finally, because humans are fundamentally altering resource availability in ecological systems at a global scale, this principle is critical for understanding how global change is likely to affect ecological pattern and process in the future (Smith et al. 2009).

3. *Biotic and biogeochemical processes are coupled through ecological stoichiometry*.—Organisms are characterized and constrained by a common set of chemical requirements, as well as being composed of similar ratios of essential elements (Redfield 1958). How these elemental ratios (i.e., stoichiometry) affect ecological processes is a key principle for understanding pattern and process from the cellular to the global scale. Species differences in their ability to acquire, allocate and store, and compete for these elements contribute to their relative success in particular environments, as well as patterns of their distribution. Perhaps of equal importance, stoichiometric requirements determine the degree to which the biota will alter biogeochemical cycles and their physio-chemical environment (Reiners 1986). Recognizing this biotic-environment feedback is critical to the most pressing issues in global change ecology today.

4. *Evolutionary history constrains the ecological present and future*.—Evolutionary history and its product, the current genetic structure of the biota, influences and constrains contemporary ecological phenomenon, and hence, the ecological future (Gould and Lewontin 1979, Cavender-Bares et al. 2009). Given sufficient time and similar selective backgrounds, convergent evolution may operate to result in equivalent ecological patterns and processes being manifest across great distances, but well-known evolutionary mechanisms (e.g., bottlenecks, founder effects, drift) will leave a legacy imprint on contemporary ecological pattern and process. The importance of the relationship between ecology and evolution has long been recognized with Hutchinson's (1965) book "The Ecological Theater and the Evolutionary Play" standing as a reminder of this principle for earlier generations of ecologists. Today, accounting for phylogenetic history and the imprint of the evolutionary past have resulted in the re-interpretation of even the most well-known and accepted patterns in ecology (Taylor et al. 2010), as well as re-affirming the importance of feedbacks between ecological and evolutionary processes (Cavender-Bares et al. 2009).

5. *Ecological history and context further increase the contingent nature of ecological systems*.—In addition to evolutionary history (Principle 4), a wide variety of other antecedent biotic or abiotic events (including geologic) affect most contemporary ecological systems and processes, often in unpredictable ways (Wallington et al. 2005). The strength of such legacy effects is not directly proportional to the time since the event occurred since the influences of some events may be muted with time, whereas others are reinforced. Most ecologists have dealt with a plot or replicate or year in a multi-year study that behaves much differently from the rest, likely due to historical context in general or some known or unknown specific event in the past. Biogeography is an outgrowth of Principles 4 and 5 (Wiens and Donoghue 2004).

6. *All aspects of ecology are scale dependent*.—Ecological systems, processes and interactions, and the physio-chemical rules that govern them,

are scale dependent at the level of the observer, the pattern observed, and the process (or mechanism) of interest. Further, different scales of processes often interact—in some cases amplifying effects, moderating in others, or even overwhelming processes at other scales (Ricklefs 1987, Peters et al. 2006). An effective way to teach this principle is by discussing examples of where altering the scale of measurement alters the conclusion of ecological research, and the consequences of incorrectly matching the scale of data collection and the research question.

7. Ecology is the science of interactions and multiple causal factors.—Ecology is, by most definitions, the study of interactions. In almost all cases, the determinants of ecological pattern and process are multiple, interactive and probabilistic—temporally and spatially. Many an ecologist has noted that isolating objects of study from these interactions, an extreme reductionist approach, severely limits our understanding and can limit the relevance of our research (Lockwood 2007). Emphasizing through examples that ecological systems and processes are affected by multiple, concurrently acting abiotic and biotic (including human) factors that are inherently interactive and variable in nature is important for communicating this principle. Indeed, research approaches that search for a single factor to explain patterns, or those that seek to ask "Is factor A *or* B responsible for pattern X", seldom provide the insight necessary for a deep understanding of the phenomenon—since often the answer is "both A and B are important." Instead, it is the relative importance of these factors, and the conditions under which their importance varies that provides the most predictive capability. As a result, there is growing recognition that ecological questions are best addressed in a multiple hypothesis and model selection framework rather than null hypotheses testing (Hobbs and Hilborn 2006, Elliot and Brook 2007). To understand the complexity that arises from this principle, students must also realize that that the statistical distributions of many of these factors are often not normal nor does their frequency directly relate to their importance. Thus, rare events can be disproportionately important in ecological systems, and uncommon organisms can strongly influence pattern and process (concepts of keystone species, ecosystem engineers, etc. are important here).

As noted above, many of these principles are not unique to ecology, and given that ecology is by design interdisciplinary and derived from so many other disciplines, we should not strive to be unique. But in total, incorporating these principles into students' mental model of our science can lead to a much deeper understanding of ecological systems. This is possible because principles such as these provide a conceptual basis for the most essential and consistent features of the behavior of ecological systems, processes, and interactions. For example, the attributes, dynamics, and interactions of organisms and ecological systems, are ultimately constrained by Principles 1–3, whereas variability, stochasticity, and unpredictability (both real and perceived) in ecological systems are predicted by Principles 4–7.

The product of these principles is that predictability and generality in ecology will be limited to specific scales and will be contingent on the past as well as the statistical distribution of contemporary variables. For example, if stochastic disturbance regimes are a key driver of the dynamics of a process or pattern, then ecological forecasts will have to reflect this. Predictability is most likely to emerge when scale is specified and appropriate, the evolutionary and ecological past can be controlled or at least accounted for, and the statistical distributions of key driving variables are known. As a result, the lack of generality and predictability that many bemoan in ecology is not something ecologists should be attempting to overcome. Rather, these attributes are essential features of a more contemporary, non-equilibrium perspective of ecological systems (Moore et al. 2009).

Using Principles for More Effective Teaching of Ecology

Constructing a concise set of ecological principles that captures one's mental construct can be challenging to be sure, but using them effectively in ecology courses is even harder. How might your teaching be different if you had an explicit set of principles in mind? How do you know whether students actually understand the principles and can apply them in their own research?

Does an emphasis on principles help students know ecological content better? The suggestions below address these and other pedagogical issues. As with the seven principles, our intention is not to prescribe "how to teach ecology". Instead, the ideas and recommendations below are designed to stimulate faculty to think more deeply about the teaching and learning of ecology so that they can develop effective courses for their own students.

Recommendations and justifications

1. *Identify and articulate your own set of ecological principles*.—It is important that each faculty member: (1) develop and write down their own set of principles and (2) repeatedly explain, refer to, and/or have students discuss these principles throughout a course, even if they are not formally labeled as such. The first step is critical because faculty from different sub-disciplines of ecology (classically population vs. ecosystem ecologists) will probably emphasize different foundational ideas and ways of thinking; therefore, a teacher cannot just verbatim use someone else's list of principles. In addition, this initial step forces a professor to "put to paper" the essential, overarching concepts and assumptions in the mental models they use, perhaps unconsciously, when presented with an ecological problem or question. The process of formally stating them also helps one more clearly describe and explain their thinking, which in turn helps them talk about the ideas more effectively in class or to the general public.

Justification.—Earlier we proposed that faculty have mental models or constructs that they may rarely explore with their students. Some cognitive researchers who study how experts and novices solve problems in scientific domains refer to experts' routine use of "internal schema" organized by the key principles in their discipline (e.g., Chi et al. 1981). This research indicates, for example, that physics experts tend to categorize problems by the major principles used in a solution (e.g., conservation of energy), while novices categorize problems by superficial characteristics (e.g., an inclined plane problem). Applying this work to classroom teaching, if a faculty member does not clearly explain their thinking about ecological principles examined in an investigation, for instance, students may fail to see the big picture and the underlying principles a professor assumes they understand. To illustrate, students with little understanding of ecological stoichiometry will likely not follow a faculty member's explanation of the interplay between diversity and nutrient dynamics in a field study, and may focus on superficial features instead (Fig. 1). In this example, while the faculty member discusses the research in the context of stoichiometry, evolutionary contingency and scale dependence, some students may focus on descriptive aspects of the study such as time of year or organisms typical in grasslands.

2. *Design an interactive class*.—Use active-teaching approaches so that students actively talk about ideas, ask you and each other questions, pose experimental designs to test hypotheses, and so on—and use limited lecture time effectively (D'Avanzo 2003). To help students' understanding of key principles, for instance, once students have grappled with challenging ideas in papers during class discussion or in homework assignments, use mini-lectures to synthesize the information and clarify the foundational ideas and thinking.

Justification.—Many studies show that students learn scientific concepts better in courses that emphasize student-active teaching (e.g., students talking to each other about a question) compared to more traditional lecture-only courses (Bransford et al. 1999). For example, Knight and Wood (2005) compared their own biology students' performance on pre-post tests and homework problems in large courses with and without active student participation and cooperative learning during class time. In repeated years, they measured significantly higher learning gains and better conceptual understanding in the more interactive course. Graduate level courses in ecology are usually 'active' since students typically discuss research articles, experimental designs, and related topics. In contrast, teachers of undergraduates are often challenged by large class sizes, students who fear or are inexperienced with discussion, and the pressure to "cover material" by colleagues and graduate school preparation. Ecology faculty can find examples of active teaching ideas and approaches for a range of class sizes in *Teaching Issues and Experiments in Ecology* (*TIEE*; ⟨http://tiee.ecoed.net/⟩).

BIODIVERSITY ⟷ NUTRIENT DYNAMICS

NOVICE'S UNDERSTANDING

Grassland ecology
Nitrogen and phosphorus cycle
Winter vs. summer
Grasses, forbs, microbes

EXPERT'S UNDERSTANDING

Principles	**Concepts**
Ecological Stoichiometry	*Relative resource allocation*
Evolutionary History	*Functional groups*
Scale Dependence	*Time/Space*

Fig. 1. Illustrative comparison of how an ecology experts' and novices' mental characterizations might differ for a study about relationships between functional plant group richness in a serpentine grassland and nutrient cycling (Hooper and Vitousek 1998). In this example, novice students focus on descriptive aspects of the study such as "grassland ecology" or "nitrogen cycle" while the expert faculty member interprets the research in the context of principles such as stoichiometry, phylogenetic constraints and the scale of the study.

3. *Develop ways to assess students' understanding of principles, concepts, information, and ideas.*—Faculty who identify outcomes for their students such as being able to "analyze, synthesize or apply" (e.g., Bloom et al. 1956) confront the problem of how they evaluate the degree to which students achieve these goals. To assess students' comprehension and application of your principles, for example, over the semester a professor could explicitly talk about—and have students discuss—principles and associated concepts they have identified by clearly linking them to papers assigned for class, an option best suited for advanced undergraduate and graduate classes. However, the principles need not be identified by 'formal' name and number. At the end of the semester, the faculty member could ask students to identify key principles in ecology, allowing ample time for students to explain their thinking verbally and in writing. When one of us (AK) does this, students inevitably re-create the instructor's list of principles; this is critical feedback that students understood these ideas.

Justification.—The National Research Council (2001) report *Knowing What Students Know* (Pellegrino et al. 2001) emphasizes the vital importance of aligning what we teach and what we wish students to learn with our measures of student performance. Thus, if a key goal in a course is that students can apply ecological principles emphasized in the course, the teacher needs to determine the best means to evaluate these abilities in ways that are appropriate and helpful for the students. For graduate students this might be accomplished by comparing/contrasting the use of these principles in research papers. Undergraduates might be asked to outline and explain concepts derived from principles in a research paper (in small classes) or write extended responses to multiple choice questions focused on principles and concepts (in large ones). In both cases, faculty should develop rubrics, or assessment criteria, for grading performance that they share with students. Communication and interactions between faculty and students thus become two-way, which is at the heart of effective pedagogy.

4. *Make complex systems understandable with everyday examples and computer simulations and models.*—Design or take advantage of learning situations that allow students to work together on engaging, real-world questions about complex systems. Jacobson (2001) explains how group discussions about ant behavior around

an anthill can help students better understand concepts such as randomness (ant movement), positive feedback loops (pheromones that point to food sources) and "self-organization from decentralized interactions" as an emergent property of the colony. Another example is use of the HubNet technology that allows students to make sense of complex systems by participating in computer simulations (Jacobson 2001). Dresner and Elser (2009) helped high school teachers develop qualitative conceptual models and reflective essays to better understand ecological complexity. Finally, graduate students and upper-level undergraduates can examine the complexity of short and long term projections of climate change effects with computer modeling.

Justification.—Education research on teaching and learning of complex systems is well grounded in constructivism (i.e., the idea that people construct understanding through active experience and refection) and cooperative learning, among other theories. For example, to help students move beyond "determinist-centralized mindsets" Wilensky and Resnick (1999) actively engaged young students in participatory simulations in which they acted out the roles of system elements and then in groups reflected on their learning. However, Hmelo-Silver and Azevedo (2006) cautions us to recognize the great challenges in teaching and learning about complex systems, noting that we are just beginning to study how people think and learn about such systems.

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Appendix

Selected examples of discussions of and efforts to identify ecological laws, theories, and principles in the ecological literature.

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