

The ecological literature, an idea-free distribution

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INTRODUCTION

Ecology is awash with theory, but everywhere the literature is bereft. Many papers in ecology do not even reference their theoretical context, while only a small minority are engaged in what is supposed to be the heart of the scientific enterprise: theory testing. I will demonstrate these assertions with an analysis of the current and historical literature. First, though, let us examine the roles that theory plays in ecology, and all of science.

Theories are the way in which we organise our ideas and turn data into knowledge. They provide a means for laying bare the assumptions that underlie our models and experiments. They provide guidelines for building models (a particular kind of theory). They provide the rationale for where we look in the world and help us interpret what we see. Contrary to some claims, there is no such thing as theory-free science. All observations presuppose a theoretical context. For example, the simple act of counting individuals and assessing species diversity relies on the concepts of ‘individual’ and ‘species,’ both of which are complex ideas (e.g. Wheeler & Meier 2000; Strassmann & Queller 2010). Perhaps more importantly, our theories are what give us warrant to take what we learn in one place and apply it to another. When we begin a prairie restoration project, we rely not just on previous projects, but general knowledge about successional processes, competitive hierarchies and mutualistic interactions. When we finish our project, we can add what we have learned at this place to the general pool of knowledge through our theoretical constructs. Hence, theories allow us to generalise from specific studies to overarching concepts.

I was prompted to do a historical analysis of theory in the ecological literature because of an invitation to participate in a symposium at the annual meeting of the Ecological Society of America honouring the thirtieth anniversary of the publication of Robert McIntosh’s *The Background of Ecology* (1985, Cambridge University Press). We were asked to comment on the history of the field since that publication, and I was assigned ‘theory’. So I decided to look at the extent to which the ecological literature engages with theory. The results were better than I anticipated, but not as good as I hoped. I used the July 2012 issue of *Ecology* as my baseline, both because it was an ESA symposium, and because it was the leading, general ecology journal during most of the twentieth century.

I assigned papers to several categories: no mention of a theory in the Introduction (case studies, methods or literature reviews), mentioning a theory (theory motivated) or engaging with theory (reviews of theories, explicit tests of one or more theories, or

development of a model, theory or conceptual framework). I tried to be as generous as possible in assigning papers to the ‘theory motivated’ category. From that baseline, I went back at ten year intervals to the beginning of the journal. If a given issue did not contain at least 20 papers, I included the preceding or following issue. To insure that I was sampling the general literature, I avoided any issue that included a special topic section or symposium collection. For a historical comparison, I did a similar analysis for *The American Naturalist* and *Evolution*, journals with similarly long histories that publish widely on topics in ecology and its sister discipline of evolution. (Of the *American Naturalist* issues surveyed, 71% of the papers focused on evolution.) For a contemporary comparison, I examined the June/July issues of *Ecology Letters*, *Oikos* and *Journal of Evolutionary Biology*, the other current leading general ecology and evolution forums.

For the first half of the last century, the ecological (and evolutionary) literature for the most part consisted of descriptive case studies that did not explicitly engage with theory (Fig. 1). That changed about 50 years ago, a change that coincided with efforts by many to bring theory and models to the forefront of ecology, most notably Eugene and Howard Odum (ecosystem ecology) and Robert MacArthur and his collaborators. However, the engagement of the ecological literature with theory consistently lagged behind

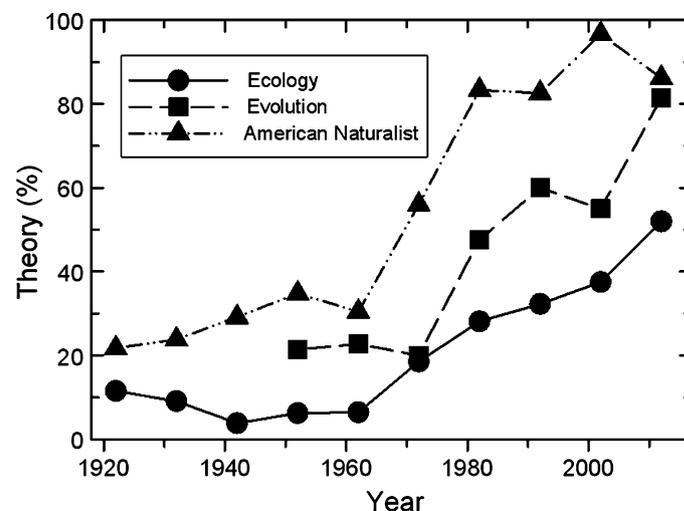


Figure 1 The percentage of papers in each journal that are either developing or testing one or more models or theories. See the online supplementary material for the details of the data (Table S1).

Table 1 A comparison of theory engagement in ecology and evolution journals for papers published in June and/or July 2012 in six leading journals, and by paper topic regardless of publication venue

By Journal	No theory			Theory motivated	Theory			% theory	95% CI
	Review	Methods	Case study		Test	Development	Review		
Ecology Letters	1	1	10	5	4	8	1	60.0%	(40.6–77.3)
Oikos	0	1	8	6	7	11	0	72.7%	(54.5–86.7)
Ecology	0	4	8	7	3	2	1	52.0%	(31.3–72.2)
American Naturalist	1	0	3	13	0	12	0	86.2%	(68.3–96.1)
Evolution	1	1	3	9	3	10	0	81.5%	(61.9–93.7)
Journal of Evolutionary Biology	0	1	6	6	5	3	0	66.7%	(43.0–85.4)
By topic									
All ecology	1	6	28	13	18	28	2	63.5%	(53.1–73.1)
All evolution	2	2	10	16	21	18	0	79.7%	(68.3–88.4)

See the online supplementary material for the details of the data (Table S1).

that of evolution. Even today, half of the papers in *Ecology* are apparently theory free. The situation is somewhat better in other journals (Table 1), but even in *Ecology Letters* 40% of the papers do not mention a theory. Even in the best ecology journal in that regard, *Oikos*, only three-quarters of the papers explicitly mention a theory. Nearly, all of these journals publish some mix of ecology and evolution. When scored by topic about 63% of ecology papers engage with theory in some fashion, as compared with 80% of evolution papers.

My indictment of the ecological literature becomes more acute when examining how those papers engage with theory. Many more papers are involved in theory development (mostly model building) than in theory testing. This is a problem. Testing an ecological theory requires many empirical studies. Ecological theories do not stand or fall on a single yes/no experimental result. In the evolutionary literature, theory tests outnumber theory development, although I am the first to admit that there are large areas of evolutionary biology where the theoretical and empirical literatures are only loosely connected (e.g. DeWitt & Scheiner 2004). Of course, the journals surveyed here are just a small slice of the entire literature. For example, there are other venues that focus on model development (e.g. *Theoretical Ecology*, *Theoretical Population Biology*). Perhaps large numbers of theory tests are occurring in other venues, which I doubt. These venues (Table 1) are the leading general journals in their fields and should be attracting the papers that are testing their theoretical underpinnings.

The empirical ecological literature must do more to engage with theory. What do I mean by ‘engaging with theory’ or ‘testing a theory’? I do not necessarily mean it in the classical Popperian sense of a false/not-false hypothesis test. That is just one small component of the wider process that takes place when we try to disprove or establish the truth of a theory. A theory consists of a set of assumptions, generalisations of facts and rules for model building. A test can include work that confirms those assumptions, generalisations of facts or rules that are currently not well supported, as well as efforts to directly disconfirm them.

By putting our research into an explicit theoretical context, we can judge how bold or risky we are being. A bolder effort addresses a broader domain or a more general theory. The least risky effort is a case study that simply solidifies an established assumption, generalisation or rule. An effort to provide additional support for one that is unconfirmed is somewhat more risky. Putting forth a new

one is even riskier, as you may be wrong. Finally, an attempt to disconfirm an established one is the riskiest strategy of all but can have a huge payoff. For example, the extremely well-established central dogma of molecular biology was that information flowed in just one direction from DNA to RNA to proteins, until the discovery of retroviruses.

Such efforts, however, require that we be explicit about what is well supported within a given theory. Support for a theory is related to its maturity, which can range from well-developed theories such as foraging theory, enemy-victim theory and island biogeography theory, to much more recent and less developed theories such as meta-community theory, global change theory and biogeographical gradient theory (Scheiner & Willig 2011b). Being explicit can help the community recognise those areas that require the greatest efforts.

Being explicit with our theories is also critical for interpreting models. Models are always simplifications. Making assumptions explicit is critical for knowing what we are leaving out of a model. For example, a fundamental principle of the theory of ecology is that the ecological properties of species are the result of evolution (Scheiner & Willig 2011a). Models of pathogen populations that also allow for evolution can show very different patterns of dynamics from those that do not (e.g. Luo & Koelle 2013). It is not that a model without evolution is wrong, just that one needs to be aware of its limitations.

Despite the many theories in ecology, much more work is needed to show how those theories can be linked to data. One way is to link particular models or disconnected theories into larger conceptual frameworks, such as those for species invasions (Gurevitch *et al.* 2011) and ecosystem services (Ringold *et al.* 2013). A framework can be turned into a structural equation meta-model (Grace *et al.* 2010) with its explicit links to data. Or the framework can form the basis of a research strategy that would provide information about the framework’s weakest links. Once assembled into a formal framework, it is much easier to make use of and see the value of individual case studies. I do not mean to imply that case studies are unimportant. They become much more valuable, however, when placed in their theoretical contexts. All of those papers that do not mention a theory are not theory free. The theory is always there and the authors need to acknowledge them.

My challenge to you is to examine the ecological literature with a critical eye towards theory engagement, especially if you are a grant

or manuscript reviewer. Be sure to be explicit about the theoretical underpinnings of your study in your next paper. Even if the goal of your paper was just to describe the properties of a particular system, making explicit the theory/theories that relates to that description will make it easier for others to use those results in either drawing generalities or describing another system. Strengthening the ecological literature by engaging with theory depends on you.

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