Against Lawton's contingency thesis, or, why the reported demise of community ecology is greatly exaggerated

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Abstract

Lawton's contingency thesis (CT) states that there are no useful generalizations ("laws") at the level of ecological communities because these systems are especially prone to contingent historical events. I argue that this influential thesis has been grounded on the wrong kind of evidence. CT is best understood in Woodward's (2010) terms as a claim about the instability of certain causal dependencies across different background conditions. A recent distinction between evolution and ecology reveals what an adequate test of Lawton's thesis would look like. To date, CT remains untested. But developments in genome-level ecology and molecular ecology point in promising directions.

1. Introduction

Ecologist J.H. Lawton has developed one of the most influential recent critiques of community ecology (Lawton 1999). His discussion is framed around the question of whether community ecology admits of “general laws.” This branch of ecology studies multi-species assemblages. It thus focuses on a level of biological organization above (single species) populations but below entire ecosystems. Lawton argued that there are no “useful generalizations” or “laws” at the community level as such. His reason is that communities are subject to a wide range of contingencies that make it impossible to generalize from one instance to the next. For example, particular communities are shaped by different geological events. They each receive a different pool of migrants in a particular order. They experience different patterns of fire, flood, storm, and so on. These one-off events can dramatically impact the composition of a community. Hence, Lawton proposes that the rules governing community composition are transitory and idiosyncratic. However, he thinks that there is hope for generality at other levels of ecological investigation. Law-like regularities obtain at the (lower) population level and at the (more inclusive) macroecological level. They are found at the population level, according to Lawton, because these systems are simpler and behave in a more uniform fashion. By contrast, at the macroecological level regional contingences become less influential. At this level, one looks at ecosystems on a broad geographic and temporal scale, “whereby a kind of statistical order emerges from the scrum” (Lawton 1999, 183). These considerations inspired Lawton to pronounce the end of community ecology as a viable discipline:

> In sum, community ecology may have the worst of all worlds. It is more complicated than population dynamics, so contingent theory does not work, or rather, the contingency is itself too complicated to be useful. But paradoxically, community ecology is not big

> and bold enough to break out of the overwhelming complexity within which it appears to be enmeshed. All this begs the question of why ecologists continue to devote so much time and effort to traditional studies in community ecology. In my view, the time has come to move on. (Ibid)

Many ecologists have heeded this suggestion. Lawton's paper has received an average of 37 citations per year since its publication, mostly endorsing his contingency thesis. Others who view their research as significant beyond the local field or stream find Lawton's conclusion unbearably pessimistic (Chave 2013). These community ecologists soldier on in the search for generality despite Lawton's warnings. Here I argue that they are correct in doing so.

Lawton's argument assumes that if a community has been influenced by unique historical events, then it cannot be explained in terms of law-like processes. I argue that this assumption is confused about the explanatory roles of ecology and history. Specifically, it views these two types of explanation as mutually exclusive. An alternative framework has recently been developed in the field of genome-level ecology (Linquist et al. 2013). To assess whether "communities" of genetic elements can be explained using models and concepts borrowed from ecology, Linquist et al. (2013) found it helpful to distinguish ecological from evolutionary modes of explanation. The key idea is that ecological and evolutionary (or historical) explanations make different idealizing assumptions about the same underlying process. In its pure form, ecological explanation treats focal entities (genetic elements, populations, communities, etc.) as static types while focusing on how their intrinsic properties interact with features of the environment. Evolutionary explanation, in its pure form, takes into account changes in focal entities over time while ignoring relations to particular features of the environment. More will be said, momentarily, about these two modes of explanation and how they are sometimes used conjointly

–such as in explanations of evolution by natural selection. The important thing to note is how this picture refutes Lawton’s argument.

A useful analogy can be drawn to the field of developmental biology. In this field, a purely genetic explanation attempts to idealize over environmental differences, while a purely environmental explanation ignores genetic differences and focus on just environmental influences. The field of genetics has moved beyond the simple-minded idea that evidence of an environmental influence negates the possibility of a genetic explanation (Sober, 2000). Rather, geneticists have developed statistical techniques for determining, given a certain pattern of variation in some trait, how much of it is explained by genetic and environmental factors, respectively. The same approach applies to historical and ecological factors and their influence on community composition. When we adopt this approach, it becomes apparent that Lawton’s contingency thesis is based on the wrong kind of data. He argues from evidence of contingency in particular communities to the conclusion that patterns of variation among communities cannot be explained by ecological laws. This would be like inferring from evidence of a genetic influence on some trait, in a particular individual, that variation among individuals cannot be explained by environmental factors. In both cases the reasoning is fallacious. Thus, it remains an open question whether, or the extent to which, ecological communities can be explained in terms of law-like relations to the environment.

This essay will proceed as follows. Section 2 offers a more precise statement of Lawton’s contingency thesis by drawing on Woodward’s (2010) concepts of stability and contingency. Section 3 reviews Lawton’s evidence for the contingency thesis. Section 4 introduces the operative distinction between ecology and evolution (or history). Section 5 applies this distinction to the community level and explains why Lawton's evidence falls short of supporting his conclusion.

2. Interpreting Lawton

Philosophers and ecologists disagree about the conditions for natural laws (Colyvan 2003; Lange 2005; Lockwood 2008). My current aim is not to wade into these disputes. Instead, I offer an interpretation of what Lawton meant by "contingent" and how to best define the field of community ecology. Clarifying these terms is a necessary first step in understanding his argument that there are no stable (or law-like) generalizations in this field.

Lawton distinguishes laws from patterns on the grounds that, "Patterns are regularities in what we observe in nature; that is, they are 'widely observable tendencies;'" whereas laws are the "general principles that underpin and create the patterns" (1999; 178). This statement suggests that Lawton views laws as causal generalizations, while patterns are mere correlations. Lawton notes that patterns can vary in their generality: "Indeed they raise the vexing problem of how many exceptions to general patterns might exist before we would no longer regard them as patterns" (ibid). A similar problem arises for laws regarding their generality. Although some interpretations of Lawton take him to view laws as universal or exceptionless (Roughgarden 2009), this would render Lawton's position rather uninteresting. Exceptions are found even in the laws of chemistry and physics (Cartwright 1983). Hence it would be no surprise to find exceptions in ecological laws also (Colyvan and Ginzburgh 2003).

Lawton's position is better stated using philosopher James Woodward's (2010) concepts of causal stability and contingency. For Woodward, causal relations are represented as counterfactual dependencies among variables. Thus, some variable Y is counterfactually dependent on another variable X just in case, for some set of background conditions B, an intervention that changes only the value of X will result in a corresponding change to Y. The stability (or contingency) of a dependency is defined by the range of background conditions (B) across which it obtains. Thus, a highly stable (for current purposes, law-like) relationship between X and Y is one that holds across a wide range of background conditions. Contingency is the opposite of stability, where a dependency is restricted to a limited range of background conditions.

These ideas are easily transferred to community ecology. Typical dependent variables (Y) in this field include species richness, average abundance, or trophic structure of a community. These are ensemble properties of multi-species assemblages. Typical independent variables (X) include the abundance of a general predator, degree of niche overlap, or other factors thought to impact a community. Background conditions (B) come in at least two dimensions: taxonomic distance (e.g. different phyla or families) and habitat type (e.g. aquatic, marine, and terrestrial habitats). Thus, in some communities it has been observed that increasing the abundance of the top predator increases the diversity of shared prey. This causal relation is stable, in Woodward's sense, to the extent that it holds true for different taxa or across different habitats. A relatively contingent ecological dependency is one that holds for few taxa or habitat types.

Lawton defines community ecology as the study of sets of coexisting species interacting at local scales. This discipline is distinct from population ecology, he claims, insofar as community ecologists study assemblages greater than just two or three species. Although some community ecologists might object to this restriction on their discipline, it is not an issue that I consider here. However, I do take exception to Lawton's requirement that community ecology studies only *local* interactions. The question of how to circumscribe communities as objects of study remains a challenging issue (Sterelny 2006). Lawton suggests that community ecology restricts its focus only to local interactions, so that processes like immigration, emigration, or other meta-community dynamics fall under the purview of macroecology. This will strike many as an artificial way to distinguish these disciplines. Community ecologists should be allowed to circumscribe the boundaries of their subject matter as they see fit and as nature dictates.

Instead of drawing the community/macroecology distinction in terms of local/non-local interactions, a more useful distinction is drawn between the kinds of processes that these disciplines investigate. Community ecologists have traditionally set aside questions about long term evolutionary processes, focusing instead on the relatively short term processes governing the abundance and distribution of species. Strategically, this simplification makes sense if it indeed turns out that evolutionary processes have only a marginal influence on community composition and abundance. Community ecologists also tend to ignore changes in community composition considered over geological time scales. Over such extended periods, community composition and dynamics are expected to vary considerably (Kricher 1998). By contrast, the macroecological perspective, which Lawton favours, takes both evolutionary and historical processes into account. As Lawton explains, “macroecology is a blend of ecology, biogeography, and evolution and seeks to get above the mind-boggling details of local community assembly to find a bigger picture” (1999, 183). My suggestion is simply that the distinction between community ecology and macroecology is best drawn by focussing on the kinds of process that these disciplines investigate. Community ecology ignores, as a simplifying assumption, evolutionary and historical changes in the focal entities that it investigates; while macroecology attempts to incorporate those changes as well as the events and processes that generate them.

This way of drawing the distinction avoids thorny issues about how to draw the boundaries around a community or what constitutes a “local” scale.

To summarize my interpretation of Lawton’s position: the counterfactual dependency relations identified for multi-species assemblages are unstable (contingent) across different background conditions such as distinct taxa and habitats. But contingency is reduced either by dropping down to the population level, or, by taking into account broad evolutionary or geological times scales. I refer to this as the *contingency thesis*.

3. Evidence for the Contingency Thesis

Lawton’s central piece of evidence in support of the contingency thesis is based on his 20 years researching a particular bracken fern community located in Skipwith, England. He explains that the relative abundances of these 17 insect species were highly predictable over short (multi-year) time periods – rare species stay rare and more common ones remain common. He adds that the composition of the community is constrained by a species of predatory ant. From Woodward’s perspective we can think of this as an invariance relation in which abundance of the predator (X) influences composition of the other members of the insect community (Y). However, Lawton suggests that this relationship is not stable across different background conditions (B).

> I observed an average of about 17 herbivorous insects feeding on bracken at Skipwith each year. Why 17? In crude order of magnitude terms, why not 2? Or 170? This most basic aspect of community structure may have surprisingly little to do with the local processes that dominate so much of traditional thinking in community ecology. (1999, 184)

Lawton goes on to identify two different types of “filter” that, he thinks, determine community composition to a greater degree than those considered by community ecologists. The first is a historical or evolutionary filter: “understanding the origins of the pool requires a knowledge of the evolutionary history of the biota, of geology, of plate tectonics, and so on” (ibid). He suggests, for example, that if members of this community had arrived in a different order it would have altered the relationship between predator and prey abundances. Lawton’s suggestion is that any number of one-off events could have significantly impacted community dynamics. Since historical events presumably differ from one community to the next, he reasons, different communities will not obey the same causal dependencies.

The second sort of filter that Lawton identifies is spatial. He proposes that local community dynamics are often influenced by such factors as their distance from a source of migration or overall meta-community structure. Lawton seems to be relying here on the aforementioned stipulation that communities are essentially local. In the previous section I argued that community ecologists are not required to restrict their focus to local species assemblages (whatever that might turn out to mean). Rather, they are free to expand or contract their field of investigation as the situation demands. Thus, if Lawton thought that the composition of his bracken fern community was largely influenced by immigration from another community down the road, he might just have considered them together as a single unit. Lawton distinguishes community ecology from macroecology in such a way that the former is limited both temporally and spatially in its purview. I argue that the field does in fact take on a different character when historical and evolutionary considerations are taken into account. But it is less committed to a particular spatial scale. Hence, we can restrict our focus to the first of Lawton’s two filters and ask whether a science of ecological communities can find generality while ignoring historical and evolutionary considerations.

4. Distinguishing Evolution from Ecology

What then is the relationship between ecology and history? For that matter, what makes a generalization *ecological* in the first place? A candidate solution to these questions has recently emerged within the field of genome-level ecology (Linquist et al. 2013). This burgeoning sub-discipline applies ecological thinking at the level of the genome, viewing families of mobile genetic elements as akin to species and stable features of the genome as their environment (Brookfield 2005). As is often the case, applying a familiar theory to a novel domain requires close attention to its core commitments. This has led to the following operational definitions of “evolution” and “ecology.”

1) A strictly evolutionary approach investigates change in some focal entity over successive generations without taking into account its relationships to particular features of the environment.
2) A strictly ecological approach assumes (for simplicity) no change in the focal entities themselves, but focuses instead on relationships between those entities and particular features of their environment.

In the following section I apply these definitions to the community level and explain how a strictly evolutionary approach is equivalent to what Lawton would classify as an historical approach. The remainder of this section explicates this distinction and shows how it can be used to determine the extent to which some patterns calls for an ecological or evolutionary explanation.

It is important to note that each mode of investigation is being defined here in its *strict* or *pure* form. This is just to say that, considered on its own, each approach makes different sorts of idealizing assumptions. For example, some of Michael Lynch's work on the evolution of genome size exemplifies a purely evolutionary approach (Lynch and Conery 2003, Lynch 2007). His "mutational hazard" model proposes that large amounts of genome evolution can be explained just in terms of mutation rate (M) and effective population size (Ne). The focal entities in this case are populations of genomes. M and Ne are independent variables that apply to intrinsic features of a genome population –they ignore relations to specific features of the environment. It is assumed that when Ne is low the influence of selection on genome evolution is negligible. This is just to say that particular features of the environment are ignored by this model under certain conditions (see Linquist et al. 2015 for a more detailed discussion). Suppose, then, that the dependent variable of interest is variation in the overall genome size across a range of eukaryotic genomes. Lynch might explain this pattern of variation by appealing to mutation rate, the length of time over which the populations have been isolated, and the respective population sizes. This would qualify as a strictly evolutionary explanation according to Definition 1, since the pattern is being explained in terms of changes in the focal entities while idealizing away from their relations to particular features of the environment.

Strictly ecological explanations are perhaps even more familiar. Ecologists routinely conduct studies of populations that focus exclusively on their relation to the environment while ignoring changes in the focal entities themselves. For example, the introduction of the Canadian beaver to Argentina in the 1940s led to a population explosion. Here the focal entity is a particular population and the relevant dependent variable is its growth rate. Ecologists attempt to determine which of several possible ecological variables (e.g. lack or predators, suitability of foliage) best explain the much higher rate of population growth in Argentina compared to North America. These studies attempt to account for differences in this dependent variable in terms of various relations to the environment. However, they do so without considering whether northern and southern populations differ genetically. That is, ecological studies tend not to consider whether there has been change in the focal entities that might account for their differential growth rates. Presumably there are good reasons for thinking, in this case, that genetic differences are negligible. The relevant point is that this mode of explanation is purely ecological in that it assumes of focal entities that they are a static type (beavers are beavers, regardless of the population) while focusing on their relation to the environment.

Of course, many patterns in nature cannot be explained either in strictly evolutionary or strictly ecological terms. Often the two types of factor interact. In these cases, it is often necessary to consider how relations between the focal entity and its environment influence subsequent changes in the entities. This would qualify as a combined, eco-evo explanation – one that incorporates both evolutionary and ecological factors. Explanations of evolution by natural section are a familiar example (e.g. Endler 1986).

Eco-evo explanations are undeniably more epistemically demanding than either pure form of explanation. For this reason it is often preferable to first establish whether a purely evolutionary or purely ecological model will account for most of the variation in some variable of interest. It is prudent to address this question before attempting to consider both evolutionary and ecological factors in conjunction. There is no need to adopt a more complicated hybrid model if a simpler model will do.

Within genome-level ecology a straightforward strategy has been developed to determine the extent to which a given pattern can be explained by ecological or evolutionary factors

(Linquist et al. 2013). One begins with a dependent variable of interest. A population of entities is then selected in which there is variation in the dependent variable. Variation in the dependent variable is required in order to determine the relative contributions of ecological and evolutionary factors. The next step is to identify independent ecological and evolutionary factors that are likely to influence the dependent variable. It is here that definitions 1 & 2 come into play. Evolutionary variables are ones that identify changes in the focal entities over time. For example, in the case of genome ecology, phylogenetic distance is used as a proxy for their evolutionary or historical divergence (ibid). Ecological variables are features of the environment thought to stand in a casual relation to the dependent variable. Admittedly, it is conceptually and empirically challenging to identify independent (ecological and evolutionary) variables that are suitable for this kind of an analysis. Those variables must themselves vary among entities in the sample population. Only then can one determine how much of the variation in the dependent variable correlates with ecological and evolutionary factors, respectively. But once the relevant variables are identified, conducting this type of analysis is a fairly simple matter of partitioning variance.

5. Identifying Generality at the Community Level

Recall that Lawton was worried about the disproportionate influence of historical “filters” on communities. He proposed that various one-off events would dramatically alter their composition and dynamics. We can think of these events as equivalent to the evolutionary factors identified in Definition 1. Imagine a community that experiences some unpredictable disruption such as a fire or flood. On the one hand, this might seem to be an ecological influence since it is externally imposed on the community. However, by hypothesis these are one-off events. Hence they cannot be treated as *variables* that take on various values across a range of communities. To treat these events in such a fashion would just be to regard them as ordinary ecological factors. To be sure, in some instances fire or flood might be viewed as quantitative ecological variables. But we are interested here in what it means for these rare events to serve as a historical filter that potentially mitigates an ecological explanation. To view these events as historical contingencies, I suggest, involves viewing them just in terms of their effects the structure of token communities and not, as it were, as general types of causes. In other words, when considering the impact of one–off events the relevant question concerns their impact on a population of communities, and not whether the event was a fire, flood, or some other factor per se. Insofar as these events have the same type of effect there is no point in distinguishing them. By analogy, Lynch's model is interested in how changes in Ne impact the fixation of alleles. It doesn't matter about which particular events lead up to a change in Ne. For explanatory purposes these "environmental" factors are treated as a generic kind of cause. Hence the explanation abstracts away from particular relationships to the environment. Much the same applies to sorts of the one-off events that Lawton was concerned about.

Let us then consider how Definitions 1 and 2 are applied to an ecological community. Suppose that the focal entities are insect communities such as the one Lawton observed. In order to conduct a regression analysis we require a population of these communities that vary in some (quantitative) dependent variable. Following Lawton, let's choose *rank abundance* as the relevant dependent variable. This standard measure in community ecology plots the relative abundances of community members against their rank in abundance, thus generating a curve with a particular shape for each community. The advantage of this as a dependent variable is that it provides a common measure for comparing taxonomically distinct communities.

Lawton’s example of predator density is a suitable independent ecological variable, provided that it also varies across the set of communities in the sample. Of course, numerous other ecological variables might be selected. It bears mentioning that there is a considerable danger of false negatives when applying this framework to test for ecological influences on some dependent variable. Unless one selects the correct independent variable(s), an ecological influence could easily be overlooked.

A greater challenge concerns the selection of historical variables. In the case of genome-level ecology, phylogenetic relatedness served as a proxy for historical or evolutionary distance. Thus, it was possible to determine how much of the variation among genomes in a sample correlates with phylogenetic distance. The problem is that prototypical communities are less cohesive than genomes. Their members move independently from one community to another. Hence one cannot easily reconstruct a phylogenetic tree for a population of communities. How then might one identify a quantitative variable to stand in for historical distance?

These limitations are indeed challenging when it comes to most *prototypical* communities. It might simply turn out that assemblages of macro flora and fauna are poor choices for testing the contingency thesis. However, recent years have seen increased interest in molecular and genome-level ecology. Diverse communities containing thousands of microorganisms can be contained in a single test tube (Swenson et al. 2000), or, in the case of gene families, uploaded to a database. These communities are easily isolated as cohesive units with divergent histories. Thus the molecular and genetic levels offer ample opportunity to test for the influence of chance historical events on (albeit unconventional) communities. With this qualification in mind we can imagine how one might test for the stability of an ecological relationship. This would involve comparing the influence of ecological and evolutionary variables across a range of different taxa and habitat types. There are a wide range of molecular and genetic systems in which these experiments could be conducted. Similarly, the dependency between predator abundance and rank abundance could be tested across a range different habitat types. Lawton’s contingency thesis would predict little stability in ecological relationships among these different types of community and distinct habitats. To date, no adequate test of this hypothesis has been conducted.

Thinking back to Lawton’s argument it becomes clear that he was in no position to pronounce the demise of community ecology. It is a straightforward fallacy to assume that the presence of a historical explanation for some particular community undermines the explanatory power of ecological laws. Nor would it make quantitative sense to ask, “How much of the Skipwith bracken fern community was determined by its historical and ecological factors, respectively?” Any given community will be influenced by both. To partition the relative contributions of ecology and history one must compare a population of communities in which there is variation in the dependent variable of interest. One also requires a way to quantify ecological and historical influences on that dependent variable. Only then, by looking for ecological correlations that obtain across a range of background conditions, can one determine the stability or contingency of an ecological dependency.

6. Conclusion

Perhaps the take-home message from this discussion is that demonstrating contingency in community ecology is no simple affair. Only certain communities will lend themselves to the kind of quantitative analysis that I have outlined. There are significant challenges associated with identifying and measuring the relevant variables. Even if one finds an apparent influence of history on the dependent variable, there will be looming questions about whether some unidentified ecological variable is perhaps being overlooked. To make matters more complex, an assessment of stability or contingency must proceed across a diverse range of taxa and habitats. In fairness to Lawton, neither the conceptual framework nor the requisite data were available at the time he was writing. However, I have suggested that recent advances in molecular and genome-level ecology make it easier to test his contingency thesis. As it stands, Lawton’s thesis has been supported by the wrong kind of data. It therefore remains an open question whether there are stable ecological generalizations at the community level.

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