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YES! THERE ARE RESILIENT GENERALIZATIONS (OR "LAWS") IN ECOLOGY

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ABSTRACT

It is often argued that ecological communities admit of no useful generalizations or "laws" because these systems are especially prone to contingent historical events. Detractors respond that this argument assumes an overly stringent definition of laws of nature. Under a more relaxed conception, it is argued that ecological laws emerge at the level of communities and elsewhere. A brief review of this debate reveals an issue with deep philosophical roots that is unlikely to be resolved by a better understanding of generalizations in ecology. We therefore propose a strategy for transforming the conceptual question about the nature of ecological laws into a set of empirically tractable hypotheses about the relative resilience of ecological generalizations across three dimensions: taxonomy, habitat type, and scale. These hypotheses are tested using a survey of 240 meta-analyses in ecology. Our central finding is that generalizations in community ecology are just as prevalent and as resilient as those in population or ecosystem ecology. These findings should help to establish community ecology as a generality-seeking science as opposed to a science of case studies. It also supports the capacity for ecologists, working at any of the three levels, to inform matters of public policy.

INTRODUCTION

OVER a decade ago ecologist J. H. Lawton (1999) asked whether there are useful generalizations or "laws" in ecology. He concluded that the answer depends on which level of biological organization one is talking about. Several meaningful generalizations were identified at the population level. However, Lawton argued that no such generalizations are forthcoming for multispecies communities. His argument was based on a handful of carefully examined communities in which locally specific factors influence species diversity. Because of the complexity of interactions within these communities, Lawton argued, historically contingent factors tend to predominate over lawlike processes. At the ecosystem level, however, Lawton proposed that a kind of "statistical order emerges from the scrum" (1999:183). It was thus recommended that ecologists searching for generality should restrict their focus either to population-level processes or to macroecological patterns. As for traditional studies in community ecology, Lawton proposed that "the time has come to move on" (1999:183).

Lawton's contingency thesis has had significant impact, both within the field of ecology and on the discipline of philosophy. In ecological journals, Lawton's (1999) paper continues to receive an average of 37 citations per year—most of them endorsing his pessimistic conclusion about community ecology. Several philosophers also regard Lawton an authoritative voice on the subject of generality in ecology (Sterenly

2001; Fenton-Glynn 2014). Other ecologists and philosophers have weighed in on the debate, either by citing examples of candidate laws (Turchin 2001; Berryman 2003; Ginzburg and Colyvan 2004), or by rejecting the concept of a law that Lawton and other skeptics employ (Cooper 1998; Colyvan and Ginzburg 2003; Lange 2005), or by taking issue with the kind of evidence used to justify Lawton's skeptical claims (Linquist 2015). This has resulted in a rather disparate body of literature often disagreeing about the nature of laws and about their existence at particular ecological levels.

Here we offer both a conceptual and an empirical critique of Lawton's thesis. A brief review of the debate over ecological laws reveals a disagreement with deep roots in the philosophy of science. We do not think that this issue can be resolved by a more thorough understanding of generality in ecology. Indeed, the conceptual dispute over the true nature of scientific laws stands as something of an obstacle to progress in this field. We therefore draw upon some recent theoretical developments that help to separate questions about the correct understanding of "law" from the question of whether there are meaningful generalizations in ecology. This framework enables us to transform Lawton's contingency thesis into a set of testable hypotheses. These hypotheses are then evaluated using a survey of 240 meta-analyses in ecology. Our central finding is that community-level generalizations are just as common and as resilient (in the sense defined below) as those at the population and ecosystem levels. This finding has important implications for the role of ecology in informing matters of public policy. It also helps to secure ecology as generality-seeking science, as opposed to a science of case studies (Shrader-Frechette and McCoy 1993; Sarkar 1996; Simberloff 2004).

REVIEW OF THE CONCEPTUAL DEBATE ABOUT ECOLOGICAL LAWS

Much of the debate over generality in ecology has focused on the conceptual question of what a law of nature is. Typically, the argument begins with a discussion of the laws of physics. Newton's first law of motion or the second law of thermodynamics are often put forward as the gold standard for laws in any discipline. As we shall soon discuss, it is difficult to say exactly what defines these as laws of nature. But the received view in the philosophy of science points to three features. First, they are *universal* in the sense of applying nearly without exception to physical systems. Second, they are *explanatory* in the sense of describing processes that underlie certain patterns in nature. Finally, these laws are thought to *predict* how physical systems would behave under a range of possible conditions. The argument against laws in ecology takes these to be necessary conditions for lawhood. Candidate ecological generalizations are then criticized for lacking one or more of the relevant properties. For example, Lawton (1999) criticizes generalizations in community ecology for being highly "contingent"—i.e., far from universal. Ghilarov (2001) makes the same criticism of generalizations in population ecology and ecosystem ecology. Lockwood (2008) argues that generalizations in population ecology lack universal scope. Peters (1991) claims that most ecological generalizations do not specify the circumstances to which they should apply, and therefore fail to satisfy the second requirement of being explanatory. Raerinne (2011) is suspicious of whether many ecological generalizations support hypothetical predictions—the third alleged requirement—because they have not been subjected to experimental manipulation.

A number of philosophers and ecologists have responded with a qualified account of natural laws. For example, Cooper (1998) claims that, unlike the laws of physics, universality is not required of generalizations in biology. Instead, he argues that ecological generalizations hold across a sufficiently large range of contexts to qualify as laws. This should come as no surprise in biology, he adds, where exceptions appear to be the norm. Colyvan and Ginzburg (2003) argue that even in physics one finds perfectly good laws that lack either universal scope, or explanatory power, or predictive accuracy. Hence these conditions are not necessary, they claim, for laws in any discipline. Along similar lines, philosopher Marc Lange (2005) argues that the generality of a law is pragmatically restricted by the explanatory aims of the relevant discipline. Physics, with its broad aim of accounting for all physical phenomena, encounters few such restrictions. Hence laws of physics are held to a high standard of generality. Ecology, by contrast, has a more limited scope. An ecological generalization qualifies as a law, based on Lange's view, provided that it remains invariant across all of the circumstances that ecology seeks to understand. Although Lange does not say where the explanatory commitments of ecology begin or end, he notes that certain systems clearly fall outside its purview. For example, generalizations in ecology do not extend to domestic collections of plants or to animals in captivity. Thus, the diversity of species found in suburban gardens or zoos do not qualify as legitimate exceptions to the species/area rule, for example (Lange 2005). Although these approaches differ in detail, they share the aim of providing an account of ecological laws that maintains for them an explanatory role while relaxing the requirement of strict universality.

Unfortunately, these amendments have failed to settle the issue. Ecologist Dale Lockwood (2008) has recently defended the universality requirement for ecological laws. He argues that the pursuit of universality is important for establishing ecology's credibility as a discipline. Government agencies often consult ecologists for guidance on matters of public policy. Lockwood worries that qualified generalizations—those admitting of various exceptions and caveats—will be ineffective in this role: "without universally true rules that can inform us on the outcome of an ecological process, ecology is limited in how much it can contribute to policy" (2008:58). Moreover, Lockwood responds that Colyvan and Ginzburg (2003) mischaracterize the true nature of laws, even in physics. Consider their example of a hailstone and a snowflake falling to Earth at different rates. Colyvan and Ginzburg (2003) argue that, strictly speaking, this system violates Galileo's law of constant acceleration. Of course, physicists usually explain this discrepancy by appealing to the influence of friction on these objects. The point is, however, that such hidden factors are routinely invoked when deriving predictions from laws. The historically most famous example of this strategy involved adding epicycles to the perihelion of planet Mercury in order to derive its orbit from the Ptolemaic model. This was a much less elegant solution than the appeal to friction in classical mechanics, but for Colyvan and Ginzburg (2003, 2010) the underlying principle is the same: if a law does not generate accurate predictions, it is always an option to posit some interfering force. The worry is that in many cases these forces are being invented just to preserve the assumption that laws are universal.

On the other hand, Lockwood (2008) argues that friction is more than just some hidden factor that compensates for the predictive shortcomings of a physical law. Instead, he views friction as a force in its own right that interacts with the laws of motion. In this view, laws of motion are universally present even when they are relatively weak and difficult to notice. In defense of this position, Lockwood argues that friction and other genuine forces stand in an additive relation to the laws of motion. That is, the fact that these forces can be summed by vector addition distinguishes them from the more ad hoc forces posited in ecology or in the Ptolemaic system. This argument has been met by Colyvan and Ginzburg (2010) who claim that many of the laws in physics are in fact nonadditive—but this is not an issue that we shall pursue further.

If a resolution to the conceptual debate about laws seems a long way off, this should come as no surprise. Without explicitly acknowledging it, this debate has followed a well-worn path in the philosophy of science. Colyvan and Ginzburg (2003) follow in the footsteps of Carl Hempel (1965, 1988), who claimed that provisos—or *ceteris paribus* conditions—are always required when deriving a concrete prediction from a law.

Provisos are statements that identify factors that potentially interfere with a system, thus preventing it from instantiating a law. For example, the second law of thermodynamics predicts an increase in entropy provided that there is no external source of energy. Open systems—those that are subject external energy sources—do not instantiate the second law. In this view, all laws that successfully explain some concrete pattern in nature must (at least implicitly) contain provisos. Laws of physics differ from laws of ecology only in the number and the kinds of provisos that they invoke. On the other hand, Lockwood (2008) follows along the path of John Stuart Mill who argued that,

> in any tolerably advanced science there is properly no such thing as an exception. What is thought to be an exception to a principle is always some other and distinct principle cutting into the former: some other force which impinges against the first force, and deflects it from its direction. There are not a *law* and an *exception* to that law—the law acting in ninety-nine cases, and the exception in one. There are two laws, each possibly acting in the whole hundred cases, and bringing about a common effect by their conjunct operation (Mill [1836] 2008:56).

This view has since come to be associated with the dispositional account of laws (Lipton 1999). It holds that laws describe the dispositional properties inherent in objects. Generally speaking, the failure of a disposition to be triggered poses no problem for its universality. For example, the generalization that all sugar cubes are soluble (a classic example of a dispositional property) might be universally true regardless of how many of those cubes come into contact with water. By the same token, laws of nature are thought to describe the inherent dispositions of systems even in cases where those tendencies are not triggered. In this view, a handful of known generalizations in physics qualify as laws, but possibly there are no universal dispositions shared by all ecological systems.

For philosophers, the debate between Hempelian and dispositional accounts is more than just a terminological dispute. The concept of a law of nature is closely bound up with notions of causality and explanation. Depending on one's views about these fundamental issues, different accounts of lawhood can appear more or less appealing. However, a solution to this debate will not come from a more thorough understanding of generalizations in ecology. Rather, it will come (if at all) by finding a reflective equilibrium among fundamental definitions in the philosophy of science. Such a solution might be a long time in coming (for a review, see Reutlinger and Unterhuber 2014). It therefore seems reasonable for an ecologist to wonder, can there be progress on the question of generality in ecology in the meantime? We certainly think so. As a matter of fact, recent developments in the philosophy of science offer guidance on this front.

Invariance and Resilience

As noted in the previous section, progress on the question of whether there is generality in ecology has been sidetracked by conceptual debates over the nature of scientific laws. We suggest separating these issues by developing an alternative framework for thinking about generality that will move the discussion forward for ecologists. Philosopher James Woodward's account of causal explanation is useful in this regard (Woodward 2003, 2010). Of central importance to the current topic are his concepts of causal stability and contingency. In Woodward's view, causal relations are understood as relations among variables. Variable Y causally depends on variable X just in case an intervention changing the value of X (and no other variable) results in a corresponding change to Y. The hallmark of a causal relation is that it remains invariant over a broad range of values (both actual and hypothetical) for X and Y. However, Woodward notes that such dependencies are always contingent on some set of background conditions. For example, striking a match at a certain rate (X) causes it to ignite (Y) only if there is sufficient oxygen in the atmosphere, if the system is sufficiently dry, and so on. Woodward uses the terms "stability" and "contingency" to describe the range of background conditions over which invariance relations obtain (see also Mitchell 2000). A relatively stable generalization holds across a broad range of background conditions; a relatively contingent one holds over a more restricted range.

In a moment we explain how these concepts help to achieve progress in debates over generality in ecology. Before doing so, a terminological issue must be addressed. In the ecological literature the word "stability" is already a source of some confusion (Grimm and Wissel 1997). This term refers to a number of different properties of ecological systems and authors are not always careful to disambiguate them. This term has not, to our knowledge, been used by ecologists to describe a property of ecological generalizations. We are therefore reluctant to introduce into the ecological literature yet another sense of "stable" that might generate further confusion. Hence we shall use "resilient" to describe the property that Woodward and others refer to as stable: that is, the tendency for a generalization to remain invariant across a range of background conditions.

Woodward's framework can be modified slightly to address the question of generality in ecology. The first thing to note is that background conditions are themselves a type of variable that can take a range of values. For instance, consider the invariance relation between striking a match and its ignition. This relation holds over different levels of atmospheric pressure, across a span of different temperatures, and so on. We can think of each type of background condition as a distinct *dimension* of resilience (Mitchell 2000). For any given generalization there will be many differed dimensions along which its resilience can be assessed. For some of those dimensions the generalization will remain relatively invariant; for others it will break down quickly. Hence, the question of whether a given ecological generalization qualifies as a "law" can now be understood as having two parts: how *invariant* the generalization is and how *resilient* is the generalization. The first question asks about the range of values over which an equation remains true for a given type of system. The second question asks about the range of different system types to which that equation truthfully applies. Ecological examples of these two parameters will be provided in the following section.

Decomposing the concept of generality into these two (more precise) notions of invariance and resilience is a step in the right direction. But it also raises a practical problem. Suppose that one aims to compare a number of candidate generalizations for their relative degrees of resilience. It would be a mistake to simply count up the number of different background conditions over which the generalizations hold. The problem is that there are indefinitely many possible parameters. For example, the invariance relation between striking a match and its ignition is resilient across different background radiation levels, at different rates of acceleration, at different points in time, and so on ad infinitum. There is also an infinite number of different background conditions across which this generalization does not hold—various altitudes on Mars, Venus, or Jupiter. Thus, any two generalizations could be made to appear more or less resilient depending on which background conditions one decides to focus. To be clear, we do not think that ecologists will, in practice, invoke such outlandish conditions when comparing the relative resilience of ecological generalizations. The important conceptual point is that they require some common measure for assessing resilience, otherwise comparisons will be meaningless.

To resolve this issue we adapt an idea from Lange's (2005) discussion of scientific laws. As mentioned earlier, Lange proposes that generality is a discipline-specific concept. Ecology, like other disciplines, is interested in certain kinds of systems and not others. According to Lange, it is no fault of an ecological law (such as the species/area rule) if it fails to describe suburban gardens and zoos. We suggest a similar approach to selecting the relevant background conditions for comparing the resilience of ecological generalizations. A limited number of background contexts can, we think, be settled upon for comparing generalizations in ecology. We do not claim that the following dimensions are exhaustive. However, our sense is that most ecologists, when confronted with a candidate generalization, will find it important to know whether it holds true for at least the following three types of background conditions. The first is taxonomic distance. Generalization A can be regarded as more *taxonomically resilient* than generalization B if it remains invariant across a broader diversity of species or higher taxa. A second dimension is habitat type. One generalization is more *habitat resilient* than another if it remains invariant across a broader set of distinct regions or biotic contexts (e.g., if it holds across both aquatic and terrestrial environments). A third relevant dimension is spatial scale. For example, a generalization might be considered *spatially resilient* if it remains invariant at the scale of whole organisms, molecular systems, and genomic communities (see Linquist et al. 2015 for an example of a spatially contingent generalization). Each of these dimensions of resilience is logically independent of the other two. Hence, a generalization might be invariant in one dimension but not others. It is therefore important for ecologists to be explicit about which dimensions a given generalization is more or less resilient.

METHODS AND PREDICTIONS

It was argued in the previous section that the question of whether there are ecological laws can be more usefully reformulated as a question about the degree to which ecological generalizations are invariant and resilient across the three relevant dimensions of taxa, habitat, and scale. In this section we apply these ideas to Lawton's hypothesis about the nonexistence of "laws" in community ecology. Recent years have seen an increase in the use of meta-analyses to test ecological hypotheses. These meta-analyses offer an opportunity to assess both the invariance and the resilience of ecological generalizations. A generalization can be regarded as invariant if a well-conducted meta-analysis identifies it as statistically significant. In other words, the generalization shows a strong likelihood of being true across a sample of different ecological studies that set out to test it. Lawton (1999) argued that invariant generalizations are more likely to emerge at the population or ecosystem levels than they are at the community level. This hypothesis predicts that a broad survey of meta-analyses in ecology would find fewer significant generalizations in community ecology compared to those identified in population or ecosystem ecology.

Lawton (1999) further hypothesized that population-level generalizations will identify causal relationships; but that higher level generalizations (if they exist) will merely identify statistical (noncausal) regularities. This hypothesis predicts that a survey of meta-analyses in ecology will find a higher proportion of causal generalizations at the population level than at community or ecosystem levels.

Our discussion in the previous section identified three dimensions of resilience that are relevant to ecology. Lawton's hypothesis predicts that generalizations in population and ecosystem ecology will be more resilient (less contingent) than generalizations in community ecology. Specifically, community-level generalizations should hold across fewer taxa, fewer habitats, and fewer spatial scales than those in population or ecosystem ecology.

To test these predictions, we undertook a survey of 240 meta-analyses compiled by Cadotte et al. (2012). This list contains a diverse sample of meta-analyses from population, community, and ecosystem ecology (in supplementary material, available at *The Quarterly Review of Biology* homepage, http://www.journal.uchicago.edu/toc/qrb/current. Prior to undertaking the survey, our responses were calibrated using a common pool of meta-analyses to help achieve concordance in our assessments. Each member of our research group then reviewed a subset of the studies in our sample. One of our team members then reviewed everyone's responses to further ensure consistency.

Of each meta-analysis we asked three questions:

1) What is the level of focus of the analysis: population, community, ecosystem?
2) Does the meta-analysis identify at least one statistically significant generalization?
3) Does each generalization identify a causal process, a statistical pattern, or a methodological question?

The following definitions informed responses to Question 1. Following Lawton, a *community-level* study was defined as one that investigates a large set of interacting species. Typical dependent variables at the community level related to biodiversity and community structure. *Population-level* studies were defined as those investigating single-species populations or two and three species interactions. Typical dependent variables at the population level included demography, physiology, distribution, and behavior. We further distinguished ecosystem ecology from community ecology by extending Lawton's discussion of whole lake manipulations and combining it with the "ecosystem" definition outlined by Carmel et al. (2013). An *ecosystem-level* study is thus one in which properties such as total biomass, productivity, or biochemical flow are summed across groups of organisms, without sensitivity to species identity. Lawton argues that this approach of collapsing multispecies variation into a few key properties, summed across species, reduces ecosystem complexity to that of a population dynamic approach. Finally, we distinguished *macroecology* as distinct from the other three levels. This category included only seven meta-analyses that looked for evolutionary processes; these studies were therefore removed from the analysis. Some meta-analyses (e.g., Wilson et al. 2006) corresponded to multiple ecological levels. In those cases, we identified for each meta-analysis the different ecological levels and, for each level, whether a statistically significant generalization was found.

Regarding Question 2, each meta-analysis publication was a single data point. A publication was classified as *general* if it identified at least one prediction that turned out to be statistically significant across the set of primary ecological studies that it reviewed. The nature and scope of each generalization was thus determined by the predictions and data within each publication in our sample. Some publications identified multiple generalizations, but these were not distinguished in our study. If a publication involved a formal meta-analysis that identified heterogeneous outcomes for prespecified groups (Gurevitch et al. 2000), it was classified as general only if the effects were in the same direction. Finally, five meta-analyses investigated methodological issues, such as the influence of experimental procedures on outcomes, and were thus removed from our investigation.

Regarding Question 3, a generalization was classified as *causal* if it identified a likely mechanism responsible for generating some pattern. Meta-analyses comparing the results of multiple ecological experiments fall into this category because the manipulation of some independent variable implies causation (Woodward 2003). A generalization was classified as statistical if it identified a general pattern without positing a mechanism. For example, a meta-analysis that identifies a phenomenological relationship between productivity and species richness is statistical, not causal.

Finally, our sample allowed us to assess resilience across two of the three ecologically relevant dimensions that were identified in the section, Invariance and Resilience. Generalizations at different levels were assessed for their taxonomic resilience by comparing the number of species and the number of phyla that were included in just those meta-analyses that identified a significant generalization. These generalizations were also assessed for their habitat stability by comparing the number of biota and the number of different sites (study locations) that were included in individual meta-analyses that identified significant generalizations. Our sample did not enable us to compare the spatial resilience of general-

TABLE 1

Ecological generalizations at different levels

Level of generality	Generalizations present	Generalizations absent	Proportion total generalizations	Proportion causal generalizations
Population	94	16	85%	93%
Community	16	7	70%	86%
Ecosystem	48	6	89%	96%

izations at the three levels because it was often impossible to classify meta-analyses into discrete categories of spatial scale.

Results and Discussion

The vast majority of meta-analyses in our sample identified significant (i.e., invariant) generalizations (see Table 1). It would appear that generality in ecology is much more pronounced than many skeptics have suggested. Nor does this generality cluster at a particular level. Although there were fewer community-level studies overall, there was no difference in the frequency of generalizations across the three categories (Fisher's exact, $P = 0.19$). Causal generalizations were also no more common at the population level than at community or ecosystem levels. Statistical (noncausal) generalizations were likewise equally distributed among levels in our sample.

Turning to our assessment of resilience, it might be expected that community or ecosystem-level meta-analyses would include a greater number of species than population-level studies. However, we found no such difference: meta-analyses that identified significant generalizations for populations contained the same number of species as those identifying significant generalizations for communities and ecosystems. However, population-level generalizations covered a narrower range of phyla than those at the community and ecosystem levels (See Figure 1A and B). Contrary to Lawton's expectations, these findings suggest that generalizations at all three levels are taxonomically resilient, with generalizations at the higher levels being slightly more so with respect to phyla.

There was no significant difference in the number of biomes covered by generalizations at the population, community, or ecosystem levels. A significant difference was detected in the number of sites represented in the meta-analyses in our sample. However, once again the trend was in the opposite direction than Lawton's contingency thesis would predict: community-level generalizations spanned a broader range of study sites than those at the population or ecosystem levels. Taken together, these findings suggest that ecological generalizations are indeed habitat-resilient, with community-level studies being slightly more habitat resilient than generalizations at population or community levels (see Figure 1C and D).

An interesting difference between this study and previous discussions of ecological laws is the large number and diversity of resilient generalizations that turned up in our analysis. Discussions of whether there are laws in ecology tend to focus on textbook examples drawn from the theoretical literature. Hence, the logistic equation (Turchin 2001; Berryman 2003) and the Lotka-Volterra predator and competition models (Turchin 2001) are popular examples of candidate ecological generalizations. Interestingly, these examples hardly made an appearance in our sample. The list of stable generalizations that did turn up is too large to describe in detail. However, a representative example reveals that the resilient generalizations, which can be shown to exist in ecology, might be quite different in character from the candidates that have, to date, dominated the philosophical discussion (see Table 2). Recent theoretical work on the selection of ecological communities suggests a potential mechanism

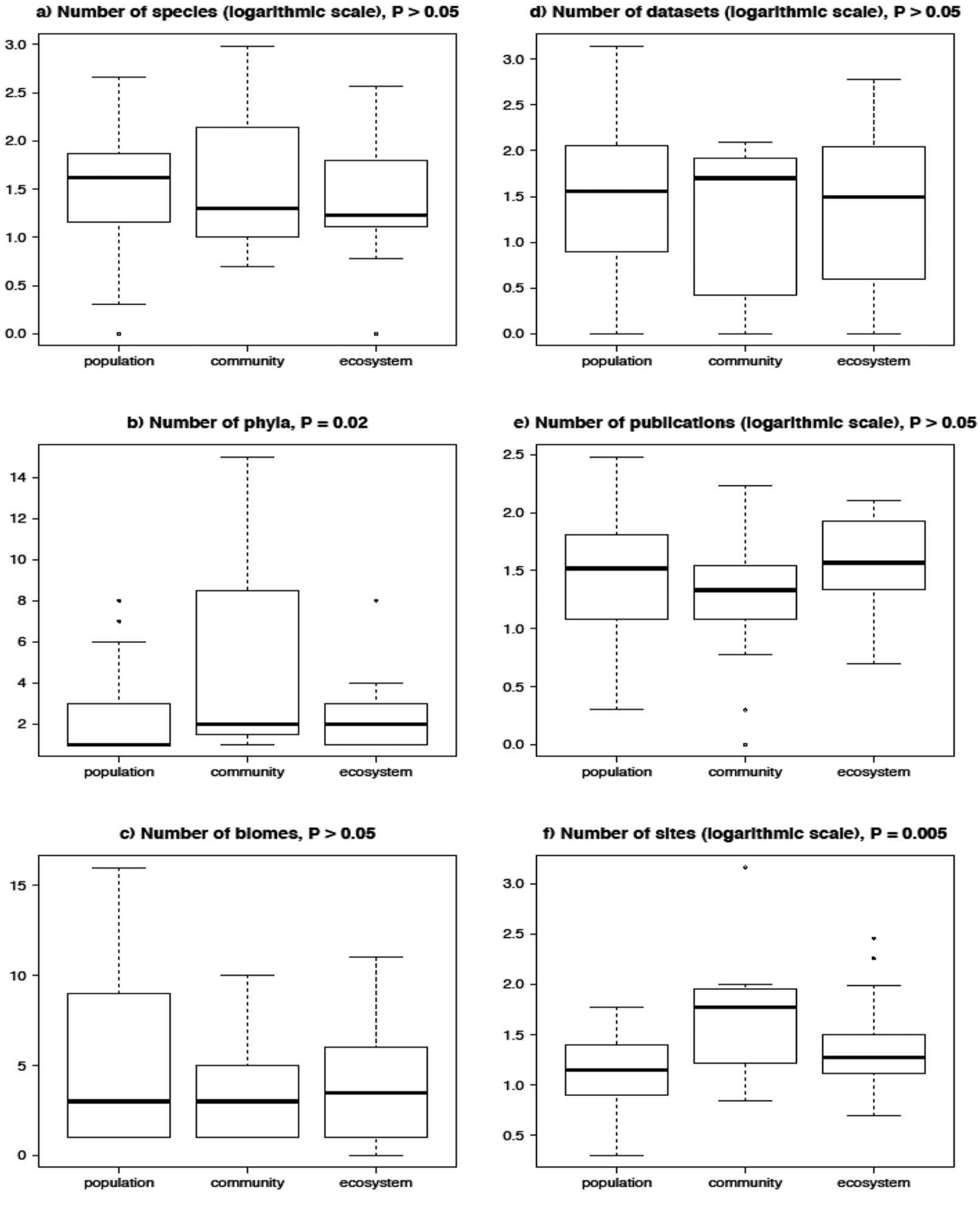

Figure 1. Dimensions of Resilience

by which some of these generalizations are maintained (Borelli et al. 2015).

A potential concern with the use of meta-analyses to test for resilience differences at different levels is that some meta-analyses might be more representative than others. In fact, our sample contained a greater number of population-level meta-analyses than community- or ecosystem-level studies. To test for level specific biases, we compared the number of publications and the number of data sets included in meta-analyses at

TABLE 2

Example generalizations in population, community, and ecosystem ecology

Level	Generalization	Stability	Author/year
Population	Habitat fragmentation negatively impacts pollination and reproduction in plants	Stable across five distinct habitats and across 89 species from 49 families	Aguilar 2006
Population	Growth, abundance, and survival of fish populations are enhanced by structured environments	Stable across four distinct habitat types	Heck et al. 2003
Community	Herbivore removal increases biomass of primary producers	Stable across marine and freshwater, but not terrestrial habitats	Gruner et al. 2008
Community	The impact of grazers on prey biomass decreases in proportion to species richness of prey communities	Stable across “a variety of habitat types” that vary in both abioic and biotic factors	Hillebrand and Cardinale 2004
Ecosystem	Plant reproduction increases with CO_2 levels	Stable across domesticated but not wild species	Jablonski et al. 2002
Ecosystem	Introduction of invasive species increases pools of stored nitrogen and carbon	Stable across 94 ecosystem studies	Liao et al. 2008

each level. There was no significant difference among the three levels of meta-analysis, indicating that no level-specific bias was present (See Figure 1E and F).

It might be further argued that this study suffers from the notorious file drawer problem (Møller and Jennions 2001). This problem can arise when negative results go unreported in primary research articles and are therefore overlooked by meta-analyses. We do not deny that a file drawer bias might have influenced the number of invariant generalizations identified in the meta-analyses that we surveyed. But there are several reasons why this possibility does not threaten our central conclusion. Our null hypothesis predicts fewer generalizations at the community level than at the population or ecosystem levels. For there to be a level specific bias, a disproportionate number of community-level studies would have to populate the drawers of ecologists’ filing cabinets. To test the representativeness of our sample we compared the distribution of meta-analyses across the three levels (population, community, and ecosystem) to a recently published survey of 750 primary research articles in ecology (Carmel et al. 2013). These single-system studies did not look for general trends. They simply reflect the distribution of research effort in ecology across the three ecological levels. If our sample is biased against meta-analyses that failed to identify generality at the community level, this should be reflected in the proportions of community-level studies in the two samples. In fact, there was no such difference. The proportions of single-system studies at the population, community, and ecosystem levels, as identified by Carmel et al. (2013), did not diverge from the proportions of corresponding meta-analyses in our sample (Fisher’s exact, P = 0.91).

Three other factors should help to mitigate worries of a file drawer bias. First, a meta-analysis that fails to identify a general pattern is no less publishable that one that does. In fact, several published meta-analyses in our sample failed to identify any significant generalization across the individual studies it analyzed. Second, the studies in our sample were not selected according to whether they identified generalizations. Rather, the sample was compiled by authors interested in the growing prevalence of meta-analyses in ecology. Finally, it should be borne in mind that Lawton’s contingency thesis makes the strong prediction that resilient generalizations will be largely absent at the community level. It strikes us as unlikely that all 16 community-level generalizations identified in our survey are the result of a file drawer bias (see Dalton et al. 2012).

Concluding Remarks

In conclusion, we respond to Lawton's question, "Are there laws in ecology?" with an emphatic "Yes!" The influence of Lawton's paper has perhaps been most profound within the discipline of ecology. Researchers in this field often cite the threat of contingency as an a priori argument against the search for generality (Simberloff 2004). Perhaps it is time for ecologists to explicitly acknowledge current practices in the discipline, which collectively point in the direction of causal generalizations at all levels. A key implication of this conclusion is that the tendency among some conservationists and policymakers to emphasize contingency (Wallington et al. 2005), while downplaying the significance of community-level generalizations, is based on incomplete evidence. Peters, another influential ecologist and philosopher, famously argued (1991) that ecology was too young a science to even bother searching for causal generalizations. Our analysis suggests that maybe it is time for ecology to undertake a more ambitious approach.

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