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Challenges of ecological complexity

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Abstract

Complexity poses enormous challenges in ecology. In order to study complexity or factor it into our theories or models, a better understanding of complexity is needed. Complexity has at least six dimensions in ecology: spatial, temporal, structural, process, behavioral, and geometric. These six sources of complexity are discussed. Issues and approaches to the study of complexity are also discussed. It is argued that our vocabulary for describing complexity is deficient in many areas. Scaling is a successful technique that has been used to simplify complex relationships. Model reduction is shown to be a powerful technique that applies when either ensembles of objects behave as aggregate wholes or conservation laws constrain overall behaviors. It is argued that experimental frames need more attention when dealing with complex ecosystem attributes. Life history theory and metapopulation models are two areas where further development of the subject depends on the ability to handle complexity properly. It is concluded that explicit study of complexity is both necessary and timely.

Keywords: Scaling; Model reduction; Experimental frames; Metapopulations; Life history theory

1. Introduction

Complexity is a tremendous challenge in the field of ecology. It impacts the development of theory, the conduct of field studies, and the practical application of ecological knowledge. Complexity is encountered at all scales, and in various guises. In this essay I attempt to characterize the types of complexity that exist, and then discuss approaches, issues needing study, and types of analyses likely to be productive.

2. Sources of complexity

Complexity in ecology is of at least six distinct types: spatial, temporal, structural, process, behavioral, and geometric. Spatial complexity has received the greatest attention because it is so visible in the forms of vegetation patterns and species distributions. In spite of this attention, our ability to describe or quantify spatial pattern is poor. Terms like “fragmentation” are subjective and not clearly related to organismal responses (e.g., [Larivière, 2003](#)).

Temporal complexity arises from population dynamics, effects of fluctuating climate and weather, and from spatial complexity. Examples include metapop-

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ulation dynamics, extinctions, invasions, succession, predator–prey cycles, etc. Temporal population fluctuations have been argued to both increase extinction risk and increase chances for coexistence.

Structural complexity refers to relationships within an ecosystem. Examples include food web structure, community composition, networks of competition, and facilitation, etc. Structural patterns must often be inferred from piecemeal observations, which leads to obvious difficulties.

Process complexity refers to processes which contain many steps or components. Examples include soil formation, the decay of logs, and succession. During the decay of a log many organisms physically alter the log in a sequential manner over a prolonged period. Succession involves facilitation, competition, immigration, changes in physical conditions (e.g., development of a litter layer), and even changes in the local climate. Piecing together the entire process is rarely easy in such cases.

Behavioral complexity is an often-overlooked aspect of overall ecosystem complexity. In contrast to the building blocks of physics, such as ideal gases and identical protons, living organisms exhibit behaviors based on the information contained in their DNA. Plants adapt their growth form to extant conditions. Animals become more adept at catching prey as they gain experience. In a few cases, models have tried to incorporate movement decisions or foraging behaviors into animal home range models, as well as in a few other contexts. Generally, however, behavioral dimensions are glossed over.

Finally, geometric aspects of ecological objects add considerable complexity to systems. An obvious example is a forest canopy or individual tree crown. This type of three-dimensional complexity is both fascinating and frustrating.

All of the types of complexity described above add cost to field studies and complicate modeling efforts. More fundamentally, since no two ecological objects (trees, frogs, tree stands, and ponds) are identical, and are located in a different spatial context, we are unlikely to be able to apply deductive methods. In building models (theories) in ecology, I would suggest that a key step is the development of basic assumptions (objects, classes, and relations), which may need to be a little more complex in order to be successful. This idea is explored next.

3. Issues and approaches

A successful attack on complexity requires a variety of approaches. In some cases, we must return to fundamentals such as classification and units of measurement. Several issues of quantification and modeling approaches are addressed next, followed by a discussion of some specific topics where complexity has hampered progress.

3.1. Vocabulary

In order to come to grips with complexity, we need a better vocabulary for spatial and temporal patterns. For example, waves of regeneration in forest are easy enough to characterize that field studies and models have been able to explain them. In contrast, differences in tree crown shape and branch architecture between species and with different growing conditions no doubt exist, but good descriptors do not exist. The difficulty here is primarily observational, because only crude measures of shape for regular crowns (e.g., cones) can currently be made. There are fractal models that generate a tree-like shape, but without good three-dimensional measurements of real trees it is not possible to say if the fractal tree is realistic. A better quantitative vocabulary is clearly needed for spatial concepts such as fragmentation, food web complexity or structure, heterogeneity, home range, etc.

In addition to a better geometric vocabulary, the fundamental units or objects of discourse need better resolution. For modeling population dynamics, it is often found that age, size, or stage structured models are necessary (e.g., for trees). That is, the simplest approach, counting the total population, may work for birds, but not when individuals vary in size by five orders of magnitude (as with trees). In this case, an increase in model complexity may be necessary to yield meaningful results. In other cases, the fundamental objects of study are not so obvious and need to be defined. For example, disturbances are not physical objects or forces, but are rather complex abstractions. The identification of such objects of study has been critical to the progress of ecology, but more care is needed on proper development and use of such objects. It is particularly important that such concepts be operationally defined so that every investigator does not mean something different when they use the terms.

An area where complexity becomes truly overwhelming is in the area of community typology. In order to study succession, environmental impact, or wildlife–habitat relations, it is often necessary to classify community types or changes in community composition over time. Different systems exist for classifying terrestrial plant communities, for example, but they are largely incommensurable, lack theoretical rigor, and are not subject to refutation. Without a rigorous typology, landscape-scale studies will remain idiosyncratic.

3.2. *Scaling*

One of the successful approaches to analyzing complexity is scaling. A scaling relation shows how a regularity or pattern exists in terms of scale. Examples include fractal models, self-thinning laws, species–area relations, and metabolic rates and home range sizes as a function of body mass.

Fractal models describe how a spatial pattern changes with scale. A self-similar fractal has the same statistical properties at multiple scales. This is a powerful model for scaling spatial pattern. More common in ecology is spatial patterns that are multifractals, in which complexity or pattern changes with scale (Loehle and Li, 1996). However, the measurement of fractal objects or patterns is far from straightforward (Loehle and Li, 1996).

It has been found that many biological processes scale with body mass (e.g., Brown et al., 2002; Linstedt and Calder, 1981). This provides a unifying framework for studying ecosystems spanning a huge range of sizes. In some cases, the geometric scaling of organisms as they grow can provide insights into processes such as self-thinning, which occurs at the population level (Li et al., 2000).

Scaling is an essential feature of key ecological variables such as species richness. The species–area curve is a fundamental feature of ecosystems that relates species richness to spatial extent. This feature is so scale-dependent that a point estimate of species richness is not even defined.

3.3. *Sampling frames*

When considering complex ecological properties, it would be beneficial to give more weight to sampling

frames. Simple physical objects need only minimal attention to the sampling frame. For example, if we wish to measure height and weight for a group of people, we have no doubt about what a person is, and height and weight have small measurement error that can essentially be ignored. In other cases measurement error is not small, but is well-behaved, and can be factored into statistical analysis. This is not true for many complex ecosystem properties. Consider food web structure, which is a rather abstract property. A food web has links that vary in magnitude. The smaller the link, the more difficult it will be to observe (Kenny and Loehle, 1991). This means that the food web structure cannot be characterized separately from the sampling intensity, and that conversion of quantitative links into binary (0–1) links will create a bias (Kenny and Loehle, 1991). Exactly the same problem bedevils attempts to quantify the number of species on a piece of ground. As more samples are taken, more species are found. If samples are spread over years, even more are found. Short of a hypothetical “complete” census, the number of species cannot be defined without considering sampling effort. When the rarest species only occur in a particular stand or pond with small probability, it is unclear what a “complete” census would even mean. Fragmentation is another concept that is sample-frame dependent. The definition of what is a gap and what is habitat has no “true” answer. Even in closed forest, if you look up there are all sorts of gaps. There are more gaps than solid vegetation. The treefall gap measured for a regeneration study is completely ignored when habitat is defined using remote sensing imagery. Without explicit consideration of sample-frame, there is an unfortunate incommensurability between studies ostensibly measuring the same thing.

3.4. *Model reduction*

If we are lucky, an ensemble of many objects may turn out to behave like a much simpler object or system. This can occur either via the law of large numbers, or via the operation of conservation laws. As an example of the first case, populations of animals often exhibit behaviors that can be replicated with fairly simple Lotka–Volterra type models, without considering space or genetics or behaviors. This is most likely in continuous habitats when the populations are not too small. A more rigorous analysis of conditions under

which such models work and when they don't would be useful.

An example of the second type is that a vegetation canopy can be represented as a big leaf for purposes of calculating photosynthesis without too much loss of accuracy. This is probably related to conservation of mass via total transpiration rates, which are limited by available water, and which are linearly related to carbon capture because water is simultaneously lost through stomates while carbon is taken up.

The degree to which ensemble behaviors are well behaved or simple is a very important factor for the progress of ecology. This aspect of the subject is not usually given formal study, which it deserves.

3.5. Life histories

Great progress was made in ecology when the distinction was made between r- and K-selected life history types (e.g., MacArthur, 1962). This classification helped clarify the nature of successional processes, for example. It has now become clear, however, that extreme exceptions exist. For example, some of the largest and longest-lived tree species are shade-intolerant and grow rapidly (e.g., redwoods). As another example, simple successional stage models clearly fail when used to explain rainforest diversity. Real life histories are clearly more complex (e.g., Loehle, 2000), and theoretical breakthroughs are needed to deal with this complexity. An explicit linkage is needed between proposed life history frameworks and growth models in terms of carbon allocation and responses to complex and dynamic environmental conditions.

3.6. Metapopulation models

Models addressing metapopulations on fragmented landscapes have both theoretical interest and practical application. There is tremendous complexity involved because both population dynamics and spatial pattern interact in this context. The impact of model assumptions is tremendous. Early percolation models, which assumed a black-and-white map and strictly local dispersal led to conclusions that are quite extreme, compared to more realistic models (e.g., Hogeweg, 1988). For example, even a very small barrier will completely prevent organism movement on a percola-

tion map (e.g., Stauffer and Aharony, 1992), but not on a real landscape. Very elaborate analyses of extinction risk have been conducted with very little feedback from experimentation. Much greater attention is needed for issues such as domain of model applicability, parameter estimation (and even estimability), and experimental testing. Complex models that have not been or cannot be tested with data should not be relied on so heavily for their management implications.

4. Conclusions

This commentary has only sought to touch on the origins of complexity and some of the issues and approaches related to the study of complexity. For many issues, such as community classification and life history theory, the ability to address complexity is fundamental to making further progress in the field. In the complex field of metapopulation dynamics, over-simplified assumptions have led to conclusions that are extreme or even false. A focus on complexity is both necessary and timely.

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