UNSOLVED PROBLEMS IN ECOLOGY

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We would like to dedicate this volume to
John Tyler Bonner,
Henry Horn,
and
Robert "Bob" May.

They each had a huge influence on each of us
and we can see signs of their huge intellectual influence
in every chapter in this volume.

The Ecosystem

Superorganism, or Collection of Individuals?

Michel Loreau

The nature of the ecosystem has been a matter of debate since its inception. When Tansley (1935) first defined the ecosystem concept, he did so in opposition to the then prevailing view of Clements (1916), who conceived plant communities as superorganisms; i.e., as higher-level biological entities that have properties of functional organization similar to those of individual organisms (Wilson and Sober 1989). According to Clements, plant communities develop regularly to a climax, just as do individual organisms to their adult stage during ontogeny. Although Tansley rejected Clements's superorganismic view, he did recognize a significant amount of organization in communities and ecosystems; he went as far as saying that "mature well-integrated plant communities . . . had enough of the characters of organisms to be considered as *quasi-organisms*, in the same way that human societies are habitually so considered [emphasis in the original]" (Tansley 1935, pp. 289–290). In contrast, Gleason developed an explicitly individualistic view of plant associations, which he regarded as the mere product of "the coincidence of environmental selection and migration over an area of recognizable extent" (Gleason 1926, p. 26).

Admittedly, the ecosystem concept has evolved substantially since the time of Clements, Gleason, and Tansley. In particular, the initial focus of ecosystem ecology on patterns of energy flow in closed systems has given way to a more dynamic view of ecosystems as open, hierarchical, spatially heterogeneous, and temporally variable complex adaptive systems (Levin 1998, O'Neill 2001). But the tension between the superorganismic and individualistic viewpoints of Clements and Gleason has nonetheless persisted to this day, and has resurfaced in various disguises throughout the history of ecology and its sister sciences.

The longstanding controversy over group selection (Wilson and Wilson 2007) is one manifestation of this tension in evolutionary biology. Indeed, pure group selection leads logically to the emergence of superorganisms (Wilson and Sober 1989). The rejection of group selection theories by many evolutionary biologists is rooted in an individualistic view of natural selection (Williams 1966), which echoes Gleason's view of plant associations.

The controversy over Lovelock's (1979) Gaia hypothesis is another manifestation of this tension. Lovelock, a geochemist, proposed that the entire Earth system behaves as a sort of superorganism, Gaia, in which organisms collectively contribute to self-regulating feedback mechanisms that keep Earth's surface environment stable and habitable for life. Evolutionary biologists such as Dawkins (1982) opposed this hypothesis based on the argument that the Earth system is not a unit of selection, and hence there is no reason why evolution should lead to a planetary environment that is favorable for life. The debate that ensued (Lenton 1998, Free and Barton 2007) is a vivid example of a dialogue where the parties have been talking past each other, which has often characterized the relationship between some branches of ecosystem ecology and biogeochemistry, which have recurrently leaned towards a superorganismic viewpoint, and a hard core of evolutionary biology, which has upheld a strict individualistic viewpoint against all odds.

The disturbing aspect of these debates is that they seem to recur without showing any sign of resolution. Yet there is ample evidence now that neither a strict superorganismic viewpoint nor a strict individualistic viewpoint hold good. These extremes distract attention from the real challenges involved in assessing the degree of integration of ecosystems and in understanding its consequences for ecosystem functioning, stability, and services in a rapidly changing world.

At one extreme, the individualistic viewpoint fails to take into account the manifold interactions that bind individual organisms to their biotic and abiotic environment and that define much of their ecology. Each living organism requires abiotic or biotic resources to stay alive, grow, and reproduce. Resource consumption inevitably leads to competition for resources among individuals, both within and between species. Consumers are themselves resources to higher-level consumers such as predators, parasites, and diseases and any leftover is recycled into inorganic nutrients by decomposers. Many organisms cooperate with other organisms from the same and other species to facilitate their access to resources, enhance their breeding success, or avoid predation. There is increasing evidence that organisms also actively modify their physical environment to meet their needs. These myriad interactions generate complex ecological networks in ecosystems, in which all organisms are inextricably embedded (Olff et al. 2009). As a consequence, each organism contributes to shaping the environment, and hence also the fitness, of other organisms, thereby becoming an actor in their ecology and evolution (Loreau 2010). Thus, there is no ground for a purely individualistic view suggesting that individual organisms behave as independent particles in some sort of inert medium.

At the other extreme, the superorganismic viewpoint fails to take into account the lability of communities and ecosystems, which generally lack clear-cut physical boundaries and show constant changes in at least part of their species composition. Ecosystem-level selection of ecosystem properties requires rather stringent conditions, in particular the existence of long-lasting and localized interactions between ecosystem components (Loreau 2010). Although some small-scale ecosystem properties may approach this ideal situation, no ecosystem in nature is so fully integrated and localized as to bypass any influence of individual selection. Therefore, it is reasonable to expect a combination of individual- and ecosystem-level selection to operate under natural conditions, with individual selection probably often prevailing as many ecological interactions are not strongly localized. As different levels of selection generally drive evolution in different directions, ecosystems are expected to evolve suboptimal properties that result from a compromise between individual- and ecosystem-level selection (Loreau 2010). As a logical consequence, ecosystems cannot be fully-fledged superorganisms.

Thus, it seems perfectly reasonable, based on existing theoretical and empirical evidence, to reject the two extreme views that ecosystems are either superorganisms or mere coincidental collections of individuals. Note, however, that even this fairly obvious conclusion still seems hard to accept for some evolutionary and ecosystem ecologists. If we accept this conclusion, the question then becomes, where do ecosystems lie along the continuum between these two extremes? To what extent are ecosystems integrated units of organization? This is a much more difficult question, to which there is probably no universal answer. Nevertheless, we might expect ecology to have accumulated enough knowledge to be able to narrow down uncertainty to some confidence interval bounded away from the two extreme viewpoints, for at least some ecosystems. The unfortunate truth is that we have no such confidence interval—which probably explains why the two extreme viewpoints resurface periodically.

There are several reasons why assessing the degree of integration of ecosystems has proved so difficult. First, the ecosystem concept is broad enough to be applied to a wide range of different systems and scales, from minute microcosms to the entire biosphere. These widely different systems are likely to show substantial differences in their functional organization and integration. Second, there was a vigorous backlash against the ecosystem concept after the initial enthusiasm for systems analysis, which views complex systems as cybernetic systems stabilized by feedback loops around a relatively constant equilibrium (Patten and Odum 1981, O'Neill 2001). This backlash resulted in a loss of interest in ecosystem ecology for some time, especially from theoretical ecologists, who, by and large, followed the new trends toward complex nonlinear dynamics and complex networks in physics and other sciences. Third, ecosystems are "medium-number systems" (O'Neill et al. 1986) that present considerable methodological difficulties. On the one hand, they are too complex to be fully accounted for by simple dynamical models (although these models have proved extremely useful to study some of their properties). On the other hand, individual organisms—the elementary particles of ecology—belong to a myriad of different species that occupy different niches, and their numbers are much smaller than those of physical particles, which precludes straightforward application of statistical approaches borrowed from thermodynamics and statistical mechanics (Loreau 2010). Therefore, there is no simple, universal approach to study and model ecosystems.

These difficulties have contributed to fuel the individualistic viewpoint, which prevails in many areas of ecology. The consequences of this state of affairs are profound, and extend way beyond a mere philosophical issue. The prevalence of the individualistic viewpoint may even be an obstacle to the discovery of ecosystem-level patterns and processes. As an example, we recently discovered general power-law relationships between prey biomass and predator biomass and between prey biomass and prey production with exponents consistently near ¾ at the scale of whole ecosystems across a wide range of terrestrial and aquatic biomes (Hatton et al. 2015). This discovery came as a surprise even to us as these robust large-scale patterns suggest that ecosystems are more tightly constrained and integrated than previously believed. Perhaps the most intriguing aspect of this finding is that ecosystem production follows the same near-¾ scaling law with biomass as does individual growth with body mass (Brown et al. 2004). Ecosystem production scaling emerges over large numbers of individuals and size structure is often near constant, indicating that similar growth dynamics at the ecosystem and individual levels arise independently (Hatton et al. 2015). Thus, similar basic processes and patterns may re-emerge across systems and levels of organization.

The mechanistic basis of these ecosystem-level patterns is still unclear, but so is the much-debated mechanistic basis of the corresponding individual-level patterns (Glazier 2010, Glazier 2015). Yet, the lack of a convincing explanation for individual-level allometries has not prevented the flourishing of a wealth of empirical and theoretical studies on this topic. One can hardly say the same for ecosystem-level patterns, which, in comparison, remain very poorly studied. One possible mechanism for the re-emergence of sublinear scaling relationships between production and biomass across levels of organization is a form of system-level density dependence in biological activity. Although density dependence has traditionally been studied as a mechanism of population regulation, interactions between individuals from different species that use shared resources might lead to stronger regulation of entire trophic levels than of their component populations, thus generating more robust patterns at the ecosystem level than at the population level. Theoretical and empirical research on this issue would be particularly exciting.

By contrast, in other areas of research, individual- and population-centered approaches have fostered the emergence of novel perspectives and understanding that might reinvigorate ecosystem ecology. For instance, they have contributed to the clarification and the resolution in large part of the long-standing controversy over the relationship between the diversity and stability of ecosystems (McCann 2000). The idea that stability emerges at the ecosystem level as a result of the diversity of population-level processes is deeply anchored in ecosystem ecology and has been central to the cybernetic approach to ecosystems (Odum 1953, Patten 1975). This tenet was overturned in the 1970s by May (1972, 1973) and others, who showed theoretically that, everything else being equal, diversity and complexity should beget instability, not stability. The fact that the stability of an ecosystem's aggregate properties may be very different from that of its component populations (May 1974) seems to have gone virtually unnoticed at that time. Only when large-scale experiments manipulating plant diversity revealed contrasting effects of species diversity on the temporal variability of population- and ecosystem-level properties such as plant biomass and production did it become clear that diversity–stability relationships were qualitatively different at the population and ecosystem levels (Tilman 1996, Tilman et al. 2006, Hector et al. 2010).

A large body of theory has subsequently been developed to identify the mechanisms by which biodiversity stabilizes ecosystem properties while at the same time often destabilizing population dynamics. A striking feature of this theory is that it uses population dynamical models to derive predictions on ecosystem stability (de Mazancourt et al. 2013, Loreau and de Mazancourt 2013), thereby establishing an explicit link between population- and ecosystem-level dynamical properties. Thus, paradoxically, population ecology has been instrumental in laying the theoretical foundations of one of the core principles of ecosystem ecology, that ecosystem stability emerges from the diversity of its component populations. This theory shows that asynchronous population fluctuations that arise from differences in the way species respond to changes in their biotic and abiotic environment are key to the stabilizing effect of biodiversity on ecosystem properties. Interestingly, deterministic differences between species' response niches provide a population-level mechanistic basis for the statistical averaging of aggregate ecosystem properties, thus linking deterministic and statistical behaviors across levels of organization (Loreau 2010). This theory has since been expanded to provide novel predictions on the spatial scaling of ecosystem stability and of its relationship with biodiversity, thus opening up a promising new area of research in ecosystem ecology (Wang and Loreau 2014, 2016).

These and other recent advances at the interface between population and ecosystem ecology show that the tension between population- and ecosystem-centered approaches in ecology can be extremely fertile if it is not congealed in opposed extreme viewpoints. Ecosystems are neither superorganisms nor mere collections of individuals; they are dynamic entities in which ecosystem-level constraints and individual-level variability interact to shape ecological patterns and processes across scales and levels of organization. The relative importance of ecosystem-level constraints and individual-level variability, however, is still a largely unsolved question. The fact that ecosystems are complex medium-number systems puts important theoretical and methodological obstacles in the way of providing a general answer to this question. Recent advances suggest that both top-down (studying whole-ecosystem patterns and processes and searching for underlying mechanisms) and bottom-up (examining the properties that emerge from the aggregation of component populations) approaches will contribute to this goal. Hopefully, narrowing the gap between these two approaches will pave the way for more integrative ecological approaches that fully account for the dynamic interplay between individuals and ecosystems.

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Untangling Food Webs

Robert M. Pringle

Just as the ecology of an organism is defined in large part by what it eats and what eats it, the properties of a community emerge largely from the network of trophic interactions among its members. Consequently, food webs are central to almost all ecological research, if not as the direct object of study then as the context in which species interactions and other processes are situated (Paine 1966, May 1983, Polis et al. 2004, McCann 2012).

But although food webs are fundamental to our understanding of ecology, we do not yet understand their most fundamental feature—the basic architecture of nodes and links that comprise the network. In vanishingly few cases and with inordinate effort, investigators have compiled something roughly approaching a complete map of trophic interactions for the set of macroscopic consumer and producer populations present at a site (Cohen et al. 2003, Brown and Gillooly 2003). But even the most finely resolved networks have missing pieces (and gaping holes if we include parasites and microbes (Lafferty et al. 2008)) and are merely static averages of what are inherently dynamic systems (Cohen et al. 2003).

Barriers to Knowing What Wild Consumers Actually Eat

Visitors to a zoo, standing in front of some big mammal from some exotic place, might field a basic question from a curious child: "What does it eat?" Although the informational placard provides only the vaguest of information ("plants"), the parents may assume that scientists know the answer. But with rare exceptions, they would be wrong. Zoo directors may appreciate the depths of our ignorance on this count better than anyone. As Mike Jordan of the Chester Zoo put it, "detailed information about the diet of the majority of free-ranging mammals and birds does not exist and often only the most generalized approximation of food items consumed is known" (Jordan 2005).

There are two major problems with the quality of empirical data used to construct food webs. First, they are poorly resolved taxonomically, with food items often lumped at the level of genus, family, or order, or else