

LINKING SPECIES AND ECOSYSTEMS: WHERE'S DARWIN?

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SUMMARY

Ecosystem ecology and evolutionary biology have traditionally been largely separate intellectual endeavors. Yet the organismal traits mechanistically responsible for many ecosystem processes result from evolutionary dynamics; those dynamics, in turn, are constrained by ecosystem processes. An understanding of evolution could enrich ecosystem studies in several ways: (1) it can provide adaptive interpretations of resource acquisition and utilization; (2) it can show how contingency and rarity limit predictability.

INTRODUCTION

Dobzhansky (1973) once famously quipped: "Nothing in biology makes sense except in the light of evolution." It is fair to say that not all ecosystem ecologists agree. Allen and Hoekstra (1992) state that though "ecosystems depend on evolved entities . . . evolution is only tenuously connected to ecosystems." Higashi and Burns (1991) likewise comment, "ecosystem ecology has virtually ignored evolutionary considerations" (see also Grimm, Ch. 1). Indeed, as a skeptical

referee of an earlier version of this chapter argued, an understanding of evolution gives no "greater insight [into ecosystems] than knowing what species are present, and what their demographic and ecosystem parameters are."

Given the few, scattered attempts to integrate evolution into ecosystem theory to date, it seems a little premature to assert that evolution should be ignored in ecosystem studies. Other authors have reflected on the need for a cross-fertilization of disciplinary perspectives. For instance, Loehle and Pechmann (1988) outlined several potential implications of evolution for ecosystem theory.

Here I revisit several of the themes of Loehle and Pechmann, and discuss several suggestive examples in which a consideration of evolutionary biology provides essential insights into an ecosystem pattern. I conclude by assessing limitations in evolutionary biology that may in some times and places circumscribe its utility in ecosystem science.

SOME BASICS

It is useful first to remind ourselves of some basic definitions. Ecosystem ecology is the study of fluxes and pools of energy and matter of all sorts (Waring, 1989; Allen and Hoekstra, 1992). Evolutionary biology in its broadest sense is the study of the origins and maintenance of biological diversity, both within lineages (microevolution, e.g., adaptation by natural selection, genetic drift), and among lineages (macroevolution, e.g., speciation, extinction, adaptive diversification, and biogeographical spread). The maintenance of phenotypic variation rests on the within-lineage processes of population genetics (e.g., sex), and the between-lineage processes of community ecology (e.g., mechanisms of local and regional coexistence).

To a reductionist, the biotic component of an ecosystem consists of individuals, which abstractly are arenas for flux and pooling in energy and materials—the fundamental resources for all life. A substantial part [though not all; see Lawton and Jones (Ch. 14) on ecological engineering] of individual organisms' roles in ecosystems is determined by their strategies for resource acquisition, retention (including the avoidance of predation, parasitism, and abiotic mortality agents), and allocation.

But resource strategies are the fruit of evolutionary processes. In some circumstances, particular species have a large effect on ecosystem function (e.g., Huntley, Ch. 8; Pollock et al., Ch. 12; Estes, Ch. 15; Wedin, Ch. 24; D'Antonio and Vitousek, 1992; Carpenter et al., 1993). I argue below that a microevolutionary perspective might sharpen our understanding of the factors determining these species' ecosystem effects.

In other circumstances, individual species effects are harder to discern (e.g., Lawton, 1990a; Lawton and Brown, 1993; Holland, Ch. 13). Microevolutionary dynamics may still be pertinent, if suites of species are collectively important and respond similarly in their phenotypic evolution to a common selective regimen (i.e., convergence) (Frost et al., Ch. 22). More generally, one must consider the full distribution among species of those characters pertinent to ecosystem dynamics. The origin of this full phenotypic distribution is explained by a blend of microevolution and macroevolutionary processes.

The traditional separation of ecosystem studies and evolution belies a fundamental dialectic: evolutionary dynamics occur within constraints set by ecosystem processes; ecosystem functions are mediated by individuals, whose traits are due to evolutionary processes. For instance, the relative selective advantage of different resource uptake strategies may be set in part by resource renewal rates (Tilman, 1988) or the total resource pool available (Holt et al., 1994); conversely, the influence of an organism on nutrient dynamics may be determined by the adaptive balance of nutrient leakage vs. storage. Articulating the reciprocal relations of evolutionary and ecosystem dynamics is a very large, and largely uncharted, piece of intellectual territory.

COMPARATIVE ECOSYSTEM STUDIES

Waring (1989) recently stressed the need for a "longer historical perspective and . . . broader geographic scale" in ecosystem studies. Evolutionary perspectives are particularly pertinent when addressing broad, comparative questions (e.g., Holling, 1992).

A tantalizing hint that evolution influences ecosystem fluxes comes from a recent worldwide comparative survey by Milchunas and Lauenroth (1993) on the effect of grazing on aboveground net primary production (ANPP). After ranking the length of the evolutionary association of large grazers and plants, these authors concluded that the percent differences in ANPP between grazed and ungrazed sites declined substantially with an increasingly long shared evolutionary history (outweighing several other factors such as short-term grazing intensity). By contrast, the effect of grazing on plant species composition increased with evolutionary history.

If one knew all the functional relationships and parameter values for species at these sites, one could quantitatively describe the ecosystem effect of grazing without explicit reference to evolution. Such a description would seem to wilfully ignore an important organizing principle that in this case simplifies our understanding of ecosystem patterns: namely, the ecosystem role of large grazers systematically varies as a function of evolutionary history. An ecosys-

tem theory incorporating evolution (via a subtheory for the coevolutionary trajectory of plant-herbivore interactions, as outlined in Milchunas et al., 1988) could be employed outside the domain of nonevolutionary theories, say to predict responses to novel environments.

MODELS OF ADAPTATION AS TOOLS IN ECOSYSTEM SCIENCE

A commonplace of evolutionary biology is that species' traits make *adaptive sense* (Williams, 1992). A detailed understanding of the adaptive nature of resource strategies (acquisition, retention, and allocation)—as governed by constraints, and played out in phylogeny—is a natural bridge linking the perspectives of evolutionary theory and ecosystem science (Loehle and Pechmann, 1988).

Species assemblages in similar physical environments, but on different continents, usually have quite different phylogenetic roots. If these ecosystems have similar structural and functional features, this similarity is likely to be due to evolutionary convergence onto comparable phenotypes from disparate ancestral phenotypes. Such convergence reflects natural selection due to commonalities in both trade-offs and the selective environment.

Tilman (1988) has argued that explicitly considering mechanistic trade-offs provides a powerful tool for interpreting interspecific interactions in communities. Such trade-offs may also be significant in determining the functional role of organisms in ecosystems (e.g., via resource uptake and retention rates).

Analyses of such trade-offs have great promise as an avenue for linking ecosystem, population, and evolutionary perspectives. Consider, for instance, the familiar correlation between vegetation defined in terms of plant life forms and climate (Colinvaux, 1993). Ecophysiological models currently provide excellent descriptors of the climatic ranges of major vegetation types (Woodward, 1987). Such models, I suggest, implicitly reflect the outcome of convergent plant evolution. Biome-level convergent evolution requires a perspective that considers biotic evolution in the context of functional constraints (O'Neill et al., 1986). It is useful to examine one biome descriptor in more detail: vegetation height.

One pattern conspicuous in forested biomes is that at any site canopy height is relatively uniform (in flat terrain), but this average vegetation height varies systematically along major physical gradients (Whittaker, 1973). Because similar patterns arise on different continents with phylogenetically distinct floras, this appears to be convergent evolution at the scale of entire biomes. Aboveground biomass increases with canopy height. Moreover, plant size is a major determinant of plant effects on ecosystems through its control of energy exchange, material fluxes, and responses to disturbance (Chapin, 1993). A

quantitative explanation of regional and global variation in vegetation height thus has major implications for terrestrial ecosystem science.

A first step toward such an explanation has been provided by King (1990; see also Givnish, 1988; Friend, 1993), who used a game-theoretical model to predict (with some success) tree height in even-aged monospecific forests. The heart of the model is the trade-off between the competitive advantage of height in competition for light, and the costs of building and maintaining higher stems. One prediction directly pertinent to ecosystem ecology is that the evolutionarily stable optimal height is not the height that maximizes the collective biomass production of a stand. I consider this model to be a nice example of how a consideration of evolutionary dynamics can be used to sharpen our understanding of ecosystem structure and function.

Comparable theoretical insights could be sought whenever a single, focal species (or suite of similar species) has a substantial impact on ecosystem processes via the use, retention, or allocation of resources. For instance, there is increasing evidence that plant species can exert a strong effect on nutrient cycling [see, e.g., Canham and Pacala (Ch. 9); Wedin (Ch. 24)]. Plants in low-nutrient environments allocate disproportionately to roots, have relative low growth rates, use nutrients efficiently, and have high carbon (C)/nitrogen (N) ratios (Hobbie, 1992). Tissues are well protected by secondary metabolites from herbivory, reducing energy flow to higher trophic levels; as an incidental byproduct, these compounds are antimicrobial agents, so litter decomposes gradually. These plant attributes generate positive feedback, accentuating soil nutrient poverty (Hobbie, 1992). The plants occupying these habitats have diverse phylogenetic origins, so this adaptive syndrome once again is an expression of convergent evolution (combined with species sorting). It would be useful to have an evolutionary strategy model (e.g., building on Tilman's ALLOCATE model, Tilman, 1988), comparable in spirit to the plant height model of King (1990), in order to predict quantitatively the combination of plant traits likely to prevail in a given environment. Such a model, to account for existing data, would have to include feedback effects via ecosystem processes.

The ecosystem role of some dominant species may also make them significant components of the selective environment faced by other species. The long-term effect of a focal species [with or without feedback on itself—Lawton and Jones (Ch. 14)] on an ecosystem may be modulated by the evolutionary responses of other species.

This may not seem important if one focuses on a single system over short periods of time, but could be crucial in understanding differences among systems, or one system over long time spans. James Estes (pers. comm.; P.D. Steinberg, J.A. Estes, and F.C. Winter, unpublished) has described a fascinating, plausible example. Sea otter predation is an important determinant of

the structure of nearshore marine communities in the North Pacific. Where sea otters are abundant, their preferred prey (invertebrate herbivores, e.g., sea urchins) are scarce, allowing the establishment of luxurious algal beds. Detrital flows from these beds help sustain rich offshore fish populations.

The abiotic environment of the North Pacific is replicated in the South Pacific (e.g., Chilean coasts). But sea otters (and any comparable species) are absent. Herbivore pressure is demonstrably higher in the South Pacific than in the North. This contrast in ecosystems has likely existed as long as sea otters have occupied the North Pacific [one reasonable guess is 10 million years (R. Hoffman, pers. comm.)], generating comparable differences in the magnitude of selection on seaweeds for mechanisms to reduce herbivory by invertebrate grazers.

Estes and his co-workers measured the levels of secondary defensive compounds in algae and found the levels to be much greater in the South Pacific than in the North. He suggests this is an evolutionary response by the algal community to sustained differences in herbivory, and that this evolutionary difference could have substantial consequences for ecosystem processes. In terrestrial ecosystems, as noted above, enhanced allocation of plant resources to secondary compounds can reduce primary productivity; moreover, plant compounds that reduce digestibility often deter decomposition, reducing flows through detrital food chains (Chapin, 1993). One might predict that otherwise similar ecosystems in the South and North Pacific might vary in the same direction, with lower productivity and reduced energy flows via detrital fluxes to offshore environments in the former.

Data are not yet available to test these predictions. But this scenario provides an example of how a consideration of evolutionary biology (namely, cascading evolutionary effects due to the presence or absence of a single, dominant species) can lead to testable ecosystem-level hypotheses.

LIMITS TO THE USE OF EVOLUTIONARY BIOLOGY IN ECOSYSTEM SCIENCE

I do not want to leave the reader with the impression that evolutionary processes are a necessary ingredient in all ecosystem studies. There are some clear circumstances when evolutionary perspectives would not appear to be very useful. For instance, if a community were comprised of species assembled hodge-podge, without prior contact (as on some islands heavily disturbed by humans), a purely phenetic approach would seem to suffice. As a second example, if an organism is an ecological engineer (*sensu* Lawton and Jones, Ch. 14) but experiences little or no feedback from its effects on the ecosystem to its own fitness, there would be a decoupling of ecosystem effect from organismal fitness (in contrast to, say, nutrient uptake).

Moreover, there are limitations to our current understanding of evolutionary mechanisms. In particular, even if one subscribes wholeheartedly to the adaptationist program, one cannot ignore the fact that evolution is also highly *contingent*: evolution works in a blindly local sense with the materials at hand (Dawkins, 1987), constrained by a phylogenetic history that itself recursively reflects the past contingency of evolutionary dynamics (for different perspectives on evolutionary contingency, see, e.g., Ulanowicz, 1986; Kauffman, 1993; Brown, 1994b). If particular species play a dominant role in some ecosystem function, the vagaries of dispersal histories will usually restrict these species (except *Homo sapiens*, alas) to particular geographical regions. This introduces a substantial historical contingency into ecosystem processes.

The theme of contingency deserves a much fuller treatment.

THE IMPORTANCE OF RARITY

An important feature of both evolutionary dynamics and community processes is that mean system states may be rather poor predictors of long-term responses to change; long-term responses often involve the magnification of the frequency or abundance of initially rare, seemingly unimportant phenotypes, alleles, or species (S. Pacala, pers. comm.). For instance, Carpenter et al. (1993) note that "surprises are common in whole-lake experiments" because of the proliferation of previously rare or unknown species (see also Frost et al., Ch. 22). An important consequence of evolutionary processes for ecosystems is that evolution sets the bounds of variation, that is, the range of extreme phenotypes available both within- and among-species, and it is these extremes that, in the end, determine the long-term response of the system to an altered environment.

CONCLUSIONS

A deeper understanding of the linkage between species and ecosystems in the future will require recognition that both species and ecosystems have histories, and that these histories reflect a mixture of predictable results from general laws, and the idiosyncratic results of accidents—evolutionary contingencies. It is this blend of order and chance that makes the study of life such an endlessly satisfying endeavor. In this noble enterprise, evolutionary biology and ecosystem science should be mutually reinforcing partners.

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