Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities

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PLAYING CHUTES AND LADDERS: HETEROGENEITY AND THE RELATIVE ROLES OF BOTTOM-UP AND TOP-DOWN FORCES IN NATURAL COMMUNITIES[1]

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INTRODUCTION

Populations and communities of organisms are influenced by a host of abiotic and biotic factors. Climate, nutrients, natural enemies (including parasites and pathogens), symbionts, competitors, decomposers, resource quality and quantity, and the availability of water are among the many potential forces that determine population change and community structure. One major challenge for the discipline of ecology is to measure the relative strengths of these forces, untangle interactions among them, and so explain the patterns of animal and plant distribution and abundance that we see in nature.

Ecologists have taken many approaches to examining the factors that drive population change and community composition, from the purely empirical (e.g., Power et al. 1985, Terborgh 1988, Alford 1989, Hunter and West 1990, Tonn et al. 1990) to the purely theoretical (May 1973, Cohen and Newman 1985, Stewart-Oaten and Murdoch 1990). Both extremes have proven valuable, and often feed from each other. The construction and analysis of food webs, for example, which emerged originally as an empirical investigation of links and potential interactions among organisms (Elton 1927, Paine 1966, 1980), has developed into a prolific branch of ecological theory (DeAngelis 1975, Cohen 1978, Pimm 1982, Cohen and Newman 1985). Even the most complex models of food webs, however, have major simplifying assumptions (Cohen and Newman 1988, Paine 1988, Polis 1991) and, with a few exceptions (e.g., Kitching 1987), often ignore environmental variability altogether. Only an experimental approach

(Pimm and Kitching 1988) will ultimately determine their real value.

With a few notable exceptions (e.g., Menge 1976, Strong 1983, Power et al. 1985, Carpenter and Kitchell 1988, Karr et al. 1992), there has been little synthesis of the relative roles of different ecological forces in determining population change and community structure. Rather, there is a collection of idiosyncratic systems, with their associated protagonists, in which opposing views on the importance of particular factors are debated. The population dynamics and host plant choice of insect herbivores, for example, are either determined primarily by natural enemies (Hairston et al. 1960, Lawton and Strong 1981, Bernays and Graham 1988) or by resource limitation (Ohgushi and Sawada 1985, Schultz 1988, Price 1990), depending upon the viewpoint and preferred system of study of the researcher involved. A similar debate permeates the literature on large mammalian herbivores in grassland systems (McNaughton 1976, Sinclair 1985, deBoer and Prins 1990). There is a fundamental disagreement over whether bottom-up forces (for example, nutrient availability) or top-down forces (for example, predators) predominate in populations and communities and whether little things (Wilson 1987) or big things (Terborgh 1988) run the world.

INCORPORATING HETEROGENEITY

We should expect the relative roles of different ecological forces to vary among biological systems, and even within the same system when environmental heterogeneity is taken into account (Dunson and Travis 1991). One reason that opposing views are long-standing in the literature is that authors carry with them experience and prejudice developed from the particular organisms that they study. The classic debate over

whether abiotic or biotic factors determine animal population change, for example, may have arisen in part from the relative stability of the environments in which the protagonists chose to do their research (see for example Andrewartha and Birch 1954, Lack 1954, Huffaker and Messenger 1964). Similarly, it should be no surprise that our own work on oaks, where host plant phenology drives changes in insect abundance and community structure (Hunter and co-workers) and on willows, where host plant quality varies dramatically with extreme variability in water supply (Price and co-workers), has led us to suggest a dominant role for plant heterogeneity in insect population dynamics and community structure (Craig et al. 1986, Price and Clancy 1986, Hunter 1987, 1990, Hunter and Willmer 1989, Hunter and West 1990, Price et al. 1990).

The real issue is whether or not we can accept the fact that many ecological factors simultaneously determine the patterns we observe in natural communities (Southwood 1975, 1977b, Quinn and Dunham 1983, Courtney 1988, Leibold 1989), that the dominant forces will vary within and among systems (Karr et al. 1992), and that incorporating and measuring that variability will increase our understanding of population and community ecology. We cannot envisage a single system in which bottom-up and top-down forces act in isolation, yet synthesis on these issues in terrestrial systems is remarkably rare. Synthesis is much better developed in aquatic systems, however, and some generalizations are available. About 50% of the variation in productivity among lakes, for example, is determined from below by nutrient input, turnover time of the water, and vertical mixing (Schindler 1978, Schindler et al. 1978, Carpenter and Kitchell 1987, 1988). The other half of the variation is hypothesized to result from a "trophic cascade" by which the influence of top predators filters down through successive levels in the trophic web (Carpenter et al. 1985, Carpenter and Kitchell 1988).

One purpose of writing this paper is to suggest that a similar synthesis is long overdue in terrestrial systems, and that the synthesis must incorporate biotic and abiotic heterogeneity. While theory describing "bottom-up" and "top-down" effects in communities is quite well developed (Smith 1969, Rosenzweig 1971, Fretwell 1977, Oksanen et al. 1981, Mittelbach et al. 1988, Persson et al. 1988), most trophic interaction models treat primary producers, herbivores, and carnivores as indivisible units (see Phillips 1974 and Leibold 1989 for exceptions) and make predictions based on characteristics of food chains, such as whether the number of levels in the chain is odd or even (e.g., Smith 1969, Oksanen et al. 1981). In contrast, experimental studies, particularly in terrestrial systems, highlight the individuality of specific animal–plant interactions. Ex-

perimental biologists dwell on the peculiarities of their chosen systems, measuring features of animal–plant interactions such as the influence of gall diameter on parasitism rates (Price et al. 1980) or the effect of defoliation on leafrolling by caterpillars (Hunter 1987).

We argue in this paper that a true synthesis of the roles of "top-down" and "bottom-up" forces in terrestrial systems requires a model that encompasses heterogeneity. That heterogeneity may be expressed as differences among species within a trophic level (e.g., Leibold 1989), differences in species interactions in a changing environment (e.g., Dunson and Travis 1991), or even changes in population quality with population density (e.g., Rossiter 1991), Simply put, the identities of individual species and environmental variation are as important determinants of population and community dynamics as are the number of levels in a food chain or the position of the system along a resource gradient. We present a simple conceptual model in which the effects of ecological factors can cascade up as well as down the trophic system. Although the term "cascading upward" is an oxymoron, we use it deliberately to parallel its use by aquatic biologists describing the flow of *interactions* rather than the flow of *energy* from the top to the bottom of a trophic web. Interactions (such as those between primary producers and their symbionts) can cascade up trophic webs to determine species diversity and population dynamics at higher trophic levels. Our template model allows species at any trophic level to vary in importance and to dominate the community. In trophic webs, as in Escher paintings, flow can be upward or downward. From every intermediate level in a trophic web there are "ladders" going up and "chutes" going down, and the major players in the game are not restricted to the top or the bottom of the web.

THE MODEL

While we accept that top-down forces such as the impact of natural enemies may dominate populations and communities in some systems, whereas the influence of primary producers may dominate in others, we suggest that the relative contributions of these are most easily distinguished by superimposing their effects on a bottom-up view of trophic structure. We do not intend to undermine the power of trophic cascades down through systems from higher to lower trophic levels (Carpenter et al. 1985), but a bottom-up template seems a logical basis for our conceptual model. This emerges from the fundamental reality that the removal of higher trophic levels leaves lower levels present (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all.

A single bottom-up template, with cascading influences up the trophic web, is shown in Fig. 1a. In this

(a) NATURAL ENEMY HETEROGENEITY

HERBIVORE HETEROGENEITY

ABIOTIC HETEROGENEITY   SYMBIONTS

PLANT HETEROGENEITY

DECOMPOSER HETEROGENEITY

(b)
ABIOTIC HETEROGENEITY   SYMBIONTS

NATURAL ENEMY HETEROGENEITY

ABIOTIC HETEROGENEITY   SYMBIONTS

HERBIVORE HETEROGENEITY

ABIOTIC HETEROGENEITY   PLANT PATHOGENS   SYMBIONTS

PLANT HETEROGENEITY

ABIOTIC HETEROGENEITY   SYMBIONTS
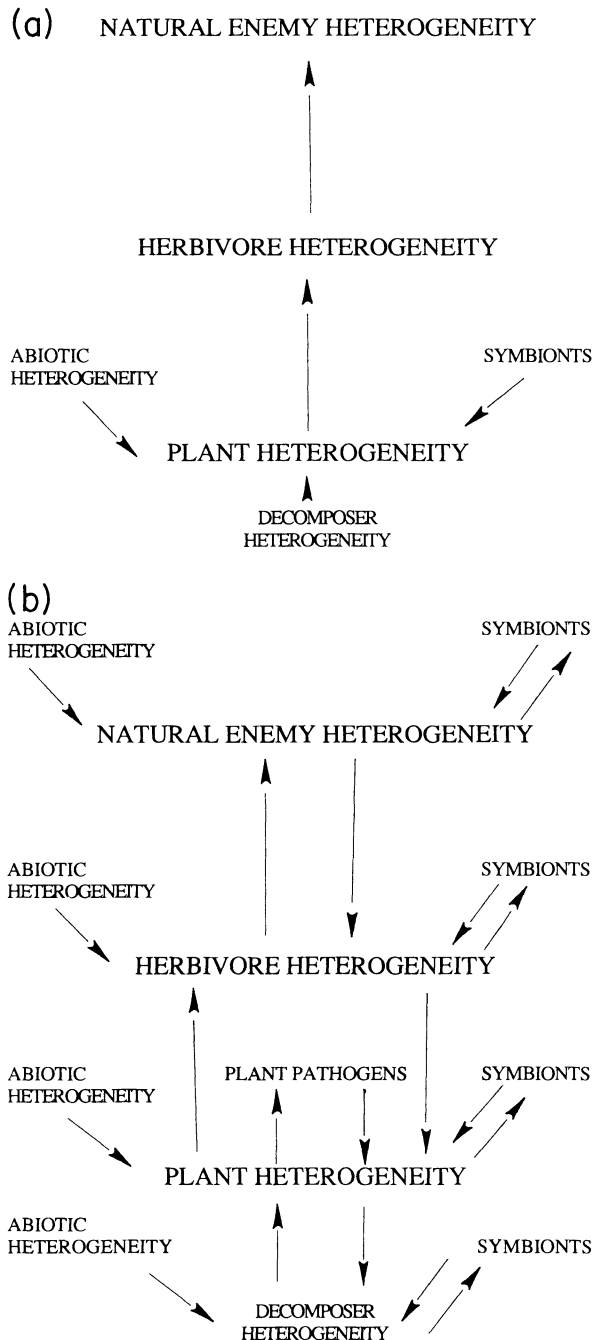
DECOMPOSER HETEROGENEITY

FIG. 1. Factors influencing population dynamics and community structure in natural systems. (a) A simple model in which variation among primary producers, determined by climate, soil parameters and symbionts, cascades up the trophic system to determine heterogeneity among herbivores and their natural enemies. (b) With the addition of feedback loops, organisms at any trophic level can influence heterogeneity at any other level by cascading effects both up and down the system.

system, variability in climate, soil parameters, decomposers, and plant–soil symbionts determines the initial heterogeneity exhibited among primary producers. Essentially, these parameters are the first to reduce the "potential" plant community to the "realized" plant community (sensu Hutchinson 1958). We include within the formation of this realized community the selection of plant parameters such as dominant growth forms, and variation in the carbon and nutrient contents of plant parts, as well as the presence or absence of particular species. This is a conscious attempt to incorporate bottom-up effects on intraspecific and interspecific heterogeneity among primary producers into the trophic system, and so differs from previous diagrammatic cascade models (e.g., Strong 1986).

Plant quality and quantity then determine the patterns of spatial and temporal heterogeneity among herbivore populations and communities. The initial carrying capacity of herbivore populations, their distributions in space and time, and the intrinsic quality of herbivores as resources for their natural enemies are seen to result from variation among the primary producers that they exploit. Heterogeneity among herbivores, in turn, determines the density, species diversity, and distribution of the first level of natural enemies, and so on up the trophic system.

The pattern described in Fig. 1a represents the template upon which the complex interactions among species in real populations and communities are superimposed. Fig. 1b adds back some level of biological reality by allowing species at each trophic level to impact those below as well as above them, and by including the effects of abiotic heterogeneity at all trophic levels. Plant diversity, for example, may depend upon the prevalence of plant pathogens in natural populations. Pathogens, therefore, may further mold the form of the "realized" plant community (cf. Price et al. 1986). Herbivores, too, can influence the quality and quantity of primary producers, and generate additional heterogeneity in the system (cf. Gilbert 1975, 1991). Likewise, the predators and parasites of herbivores are permitted to dominate the populations of primary consumers, thus releasing plants from the pressures of herbivory.

A "bottom-up template" perspective is compelling because plants form a major component of large-scale patterns over landscapes and geographic regions (e.g., Tansley 1965, Whittaker 1970). Vegetation provides the habitat template central to Southwood's (1977a) constraints on adaptation by organisms, and their responses to gradients in time and space (e.g., Southwood et al. 1983, 1986, 1988). In response to the abiotic environment, plant communities appear to produce the best understood, most general, and repeatable patterns on any landscape and in any biogeographic re-

gion. Such broad patterns best serve the development of general theory.

ADVANTAGES OF THE MODEL

Superimposing interactions among species and their environment upon a template of cascading effects up the system has several advantages. First, it permits the system to be dominated by species or guilds at any trophic level through "feedback loops." Because all members of the web are connected to each other and the abiotic environment by "chutes" and "ladders," the action of any one species (or the action of the environment on that species) can have a pervasive influence on all others. This is important because there is no theoretical reason why organisms at any trophic level should not act as keystone species (Pimm 1982). The effects of plant pathogens, for example, by determining the species diversity or biomass of primary producers (cf. Burdon 1987), or even the availability of nutrients (Matson and Boone 1984), could feed back through the system and ultimately control variability among herbivores and their natural enemies. By allowing trophic cascades both up and down the system, the model supports the recent emergence of studies of keystone species at a variety of levels in food webs (Gilbert 1980, Ehrlich and Daily 1988, Howe and Westley 1988, Terborgh 1988, Brown and Heske 1990, Kerbes et al. 1990, Hunter 1992a).

Second, the model can encompass the mechanisms of interactions (or routes of feedback) among species. It can therefore exploit the wealth of mechanistic studies that have dominated the terrestrial animal–plant literature since the 1970s. The arrow from herbivores to plants in Fig. 1b, for example, need not represent a simple change in biomass. Herbivores can influence the species diversity (Grubb 1971, Merton et al. 1976, Harper 1977, Lubchenco and Gaines 1981, Crawley 1983, Hay 1985), growth form (Whitham and Mopper 1985, Hunter 1987, Duffy and Hay 1990), phenology (Faeth 1987), chemistry (Green and Ryan 1972, Haukioja and Niemela 1977, Schultz and Baldwin 1982), and genetic diversity (Simms and Fritz 1991, Fritz and Simms 1992), of their host plants as well as simple abundance (Ross et al. 1970, Stark and Dahlsten 1970, Campbell and Sloan 1977, Louda 1982a, b). These routes of feedback allow certain keystone herbivores to change dramatically the composition of their plant community, changes that can cascade up the system, through their own trophic level, and beyond (Leibold 1989, Hunter 1992a).

A third advantage of the model is that it should focus attention on the extensive heterogeneity in natural systems (Loucks 1970, Denno and McClure 1983, Pickett and White 1985). The question "Do natural enemies or does primary productivity regulate the population dynamics of insect herbivores or African ungulates?" should become, "Under what combinations of soil conditions, plant community structure, and abiotic variability do natural enemies dominate trophic interactions?" This incorporation of heterogeneity is implicit in studies of tri-trophic interactions (Price et al. 1980, Power et al. 1985, Kareiva and Sahakian 1990, Schultz et al. 1990) where variation among plants modifies the efficacy of natural enemies, and in studies that investigate the effects of abiotic characteristics (such as pH or temperature) on interspecific competition (Dunson and Travis 1991).

DISADVANTAGES OF THE MODEL

Our model does not consider explicitly changes in community structure nor interactions among animals and their abiotic environment over evolutionary time. While the bottom-up template approach can usefully be applied, for example, to the influence of host plant patches on frugivorous mammal demographics (Fleming 1992), it does not describe the evolutionary processes that generated the frugivore–fruit interaction. Evolutionary change is a vital component of plant–animal–natural enemy interactions (Denno and McClure 1983, Strong et al. 1984) in which both bottom-up and top-down forces are active (Bernays and Graham 1988, Schultz 1988, Hunter 1990, Scriber and Lederhouse 1992). We see our model as more appropriate for an ecological time scale in which heterogeneity in natural systems generates patterns of population change and community structure rather than adaptation.

That is not to say that all the ecological forces depicted in Fig. 1b must act on exactly the same time scale. In the same way that trophic cascades (from top to bottom) and physiochemical factors act at different time scales to determine the productivity of lakes (Carpenter and Kitchell 1988), so the processes of plant succession and changing resource availability act at a different time scale from natural enemies to determine the population dynamics and community structure of insects on plants (Price 1992).

The model may be adaptable to an evolutionary perspective in the future. Plants are basic in most terrestrial food webs, and every herbivore individual in a population relates to plants most of the time. This tight linkage will have strong evolutionary consequences within the constraints imposed by phylogeny (e.g., Price et al. 1990). Enemies of herbivores may have a predictably weaker impact because some herbivores escape predators (none escape plants) and herbivores can evolve tolerance to parasites. Hence, the "bottom-up" perspective as a first approximation of real pattern in nature is likely to be fruitful for the development of evolutionary theory as well as ecological theory.

One further drawback of our approach is that it requires a greater level of understanding of the biological systems in which we conduct our research, and such information is often difficult, time-consuming, and expensive to collect. It means that plant community ecologists should not ignore the ecological impact of natural enemies cascading down the trophic system, nor should parasitoid biologists ignore variation in the soils and plant communities with which their organisms of choice are inextricably linked.

It seems to us insufficient, for example, to consider the degree to which spatial density-dependent parasitism can stabilize the populations of insect herbivores (e.g., Elkinton et al. 1990, Stewart-Oaten and Murdoch 1990) without considering the fundamental role of the host plant (such as variation in plant susceptibility) in determining the spatial distribution of the insect hosts. Spatial density-dependent parasitism cannot occur unless hosts are distributed unevenly. Differences among plants in nutritional and defensive characteristics are powerful generators of contagious herbivore distributions (Denno and McClure 1983).

We join with others, therefore, who call for a broad-based, multi-disciplinary approach to population and community ecology (Faeth 1987, Pimm and Kitching 1988, Dunson and Travis 1991, Karr et al. 1992). The success of this approach is apparent in several systems (Schindler 1978, Schindler et al. 1978, Carpenter and Kitchell 1987, 1988, Brown and Heske 1990).

EVIDENCE FOR CASCADES UP TERRESTRIAL SYSTEMS—A CASE STUDY

Our model demands that we accept the reality of cascades from lower to higher trophic levels in terrestrial systems, as is now well documented in aquatic systems (Menge 1976, Schindler 1978, Carpenter and Kitchell 1987, 1988, Leibold 1989). Studies of the pedunculate oak, *Quercus robur*, a dominant member of the deciduous forest community in much of Europe, provide an example of cascading ecological effects from the bottom up.

The budburst phenology of *Q. robur* varies between years, between sites, and between individuals in the same site (Varley and Gradwell 1968, Crawley and Akhteruzzaman 1988, Hunter 1990, Hunter 1992*b*). Variation in phenology drives the population dynamics of two spring lepidopteran defoliators on oak, *Operophtera brumata* and *Tortrix viridana* (Schutte 1957, Satchell 1962, Varley and Gradwell 1968) and usually maintains their populations below levels at which interspecific competition is severe (Hunter and Willmer 1989). When competition does occur, the greater sensitivity of *O. brumata* to budburst phenology (Hunter 1990) reverses the competitive advantage it would enjoy over *T. viridana* in the absence of phenological variation (Hunter and Willmer 1989).

Most of the natural enemies associated with *O. brumata* and *T. viridana* track the yearly changes in defoliator populations. Some passerine birds (especially *Parus* species), for example, have larger clutches in years of high defoliator density. *Operophtera brumata* abundance alone explains 47.5 and 39.3% of the variation in clutch size of *Parus major* and *Parus caeruleus*, respectively (Perrins 1990). Changes in the fledgling success of *Parus* may even influence the demographics of the Sparrow Hawk (*Accipiter nisus*; I. Newton, *personal communication*). Although some pupal predators of *O. brumata* can act in a density-dependent fashion, they are not responsible for major changes in insect abundance (Varley et al. 1973).

The cascading effects of variable budburst phenology in *Q. robur* up the trophic system are not restricted to spring. By determining the densities of *T. viridana* and *O. brumata* among trees, budburst phenology influences three guilds of late-season insect herbivores on oak through defoliation-induced changes in foliage quality, maintained from spring to fall. The effects of defoliation are generally negative for late-season leaf miners and aphids (West 1985, Silva-Bohorquez 1987), and generally positive for late-season leaf chewers (Hunter 1987), and influence their within- and between-tree distributions, the impact of their natural enemies, and their population dynamics.

On *Q. robur*, then, environmental variability among sites interacts with yearly variation in climate and genetic variation in the oak population to determine complex patterns of budburst phenology. These effects cascade up the trophic system to spring defoliators, influencing competitive interactions between them, and their effects on late-season herbivores. Patterns of herbivore abundance are then transmitted to at least one, if not two, higher trophic levels (Hunter 1992*a*).

THE GENERALITY OF A TEMPLATE/TROPHIC CASCADE MODEL

Although we developed the conceptual model presented here from our studies of insect–plant interactions, we believe that it has broad generality because it can encompass systems dominated by both top-down and bottom-up forces. The kind of bottom-up cascade at the heart of our model has been described from other terrestrial systems. For example, the population dynamics, mating systems, social organization, and migratory behavior of both microtine rodents (Ostfeld 1992) and frugivorous and nectarivorous birds and mammals (Fleming 1992) are strongly influenced by heterogeneity among primary producers.

Feedback loops, by which species or guilds at a given trophic level change the resources available for their

own trophic levels and consequently for species at higher trophic levels, have been described in rodents (Brown and Heske 1990), tortoises (Merton et al. 1976), damselfish (Hixon and Brostoff 1983), zooplankton (Leibold 1989), grazing mammals (Hutchinson and King 1980), and hippopotamus (Eltringham 1974), among others.

We concur with authors who argue that "bottom-up" and "top-down" forces act on populations and communities simultaneously, and that the dichotomy between the two forms of regulation can be artificial (Oksanen et al. 1981, Mittelbach et al. 1988, Leibold 1989). From our point of view, a much more interesting question is to what extent variation at different levels in the food chain, or in abiotic factors, can influence the relative strengths of "bottom-up" and "top-down" forces (e.g., Oksanen 1983). Some theoretical models have addressed variation in the abundance of nutrients (i.e., a resource gradient) on vertical processes in food chains (Smith 1969, Rosenzweig 1971, Wiegert 1977, Oksanen et al. 1981, Mittelbach et al. 1988, Persson et al. 1988), but such models almost exclusively ignore variation at more than one trophic level. Yet the last 20 yr of animal–plant ecology have demonstrated unequivocally that not all plants are equally edible, not all herbivores equally damaging, not all predators equally efficacious, and not all environments equally hospitable. Moreover, these heterogeneous variables interact with one another (Price et al. 1980, Karban 1989). We argue that a synthesis of "top-down" and "bottom-up" forces in populations and communities will depend upon understanding interactions between heterogeneous forces at all trophic levels.

Cataloguing the outcome of single-factor studies is not synthesis. Ecologists tend to champion their favorite ecological factor (indeed some have made careers doing so), but collecting examples of where natural enemies, climatic conditions, or primary producers dominate particular systems, and weighing their relative importance by the number of manuscripts in support of each, tells us little about the way the world works. The only way to overcome our ignorance is to pursue multi-trophic investigations (both experimental and theoretical) from the outset.

We have presented a conceptual model that we feel is a start in the right direction. Experimental biologists can proceed by measuring heterogeneity at different levels in the web, and by manipulating ecological factors, within the bounds of the heterogeneity measured, in a multi-factorial design (e.g., Karban 1989, Dunson and Travis 1991). Theoreticians must also play an important role in any synthesis, and Leibold (1989), by building on the work of Phillips (1974) and Oksanen et al. (1981), has shown that modelling complex, heterogeneous forces is a realistic goal. He argues that the

relative edibility of plants, their relative responses to limiting resources, and the type of herbivore in the community will all influence the outcome of models in which resource availability, plant susceptibility to herbivores, and predation rates are allowed to vary. The development of ratio-dependent population models, from which emerge intrinsic balance between "top-down" and "bottom-up" forces in communities (L. R. Ginzberg, *personal communication*), may also provide a valuable tool in the development of synthesis. Whatever the approach used, we must recognize that determining the relative importance of cascades up and down trophic systems will depend upon measuring and understanding heterogeneity at all trophic levels.

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