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Community Ecology: Is It Time to Move On?

(An American Society of Naturalists Presidential Address)*

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ABSTRACT: Because of the contingency and complexity of its subject matter, community ecology has few general laws. Laws and models in community ecology are highly contingent, and their domain is usually very local. This fact does not mean that community ecology is a weak science; in fact, it is the locus of exciting advances, with growing mechanistic understanding of causes, patterns, and processes. Further, traditional community ecological research, often local, experimental, and reductionist, is crucial in understanding and responding to many environmental problems, including those posed by global changes. For both scientific and societal reasons, it is not time to abandon community ecology.

Keywords: community ecology, general laws, introduced species, kelp, longleaf pine, red-cockaded woodpecker.

In a frequently cited article, John Lawton (1999, pp. 178, 183) says, "Community ecology is a mess," and "All this begs the question of why ecologists continue to devote so much time and effort to traditional studies in community ecology. In my view, the time has come to move on." By traditional community ecology, he means "experimental, highly reductionist and intensely local in focus" (Lawton 2000, p. 15). His discontent is driven by his perception that communities are too complex and contingent to permit general laws, and his recommendation is to retreat to population biology and move on to macroecology.

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There are three separate issues here. First, does community ecology really not have general laws? Second, is the worth of community ecology as a science determined by the degree to which communities adhere to general laws? Third, whether community ecology has or will ever have general laws, we must study communities because understanding them is crucial to dealing with many key conservation and environmental issues.

Science and the Importance of General Laws

The first issue of whether community ecology has general laws can be dispensed with quickly. Except for very high-level laws, such as those of thermodynamics, that are so basic as to be ecologically uninteresting, I concede Lawton's point: the "general laws" of community ecology consist of relatively few fuzzy generalizations. Some of these, for example, the frequent top-down governance of ecosystems by large carnivores, have been gleaned from excellent scientific research and may be enormously useful in management. But such generalizations all have exceptions, and their application to specific management matters requires tedious, difficult elaboration of details. Lawton's explanation for this paucity also seems correct; most communities in nature are extremely complex, so the laws are too contingent to be widely applicable. It is possible by painstaking field study to understand the processes governing local communities, but this understanding is often not very transferable, even to broadly similar systems (Lawton 2000; Hansson 2003). In fact, Lawton (1999, p. 183) sees the overwhelming emphasis on "localness" as "perhaps *the* major weakness of traditional community ecology."

However, does the absence of precise, quantitative, general laws render community ecology a weak science to be superseded? I do not believe so. Strong (1980) observed that ecology differs characteristically from physics in that physics has rather few types of fundamental units—particles—and that these differ in relatively few ways (mass,

charge, velocity, etc.). By contrast, the fundamental units of ecology—individual organisms—differ in many ways. Communities, composed of populations of different species, each itself comprising many different individuals, are vastly more variable still. It is no surprise that the complete, detailed dynamics or even the statics of communities have not been subsumed under tractable general laws, other than laws that govern their constituent elements (in the limit, the fundamental particles of physics). Lawton (1999) admits the possibility that we simply have not yet had sufficient imagination to have deduced more useful and interesting laws, but he is skeptical about our future prospects, and I agree with him. We might both be wrong. It may be that an ever-increasing catalog of detailed case studies, growing understanding of indirect interactions, and increased attention to phenomena at large spatial extents and over long timescales will lead to a set of fundamental ecological laws analogous to those of physics.

Where I disagree with Lawton is his contention that the current and possibly inherent absence of general laws makes community ecology less interesting and somehow weaker. This is part of an old, recurring complaint that ecology in general is a “soft” science (Pigliucci 2003). Windelband (1894) drew the distinction between nomothetic knowledge, which is the goal of most natural sciences and consists of general laws about the structure and workings of nature, and idiographic knowledge, which characterizes historical sciences and consists of depicting singular events in a coherent narrative focusing heavily on unique aspects of particular phenomena. Raup and Gould (1974; cf. Gould 1980) introduced these terms and this distinction to a wider audience, but the unease of biologists in general and ecologists in particular about the apparent absence of general laws in biology, that is, about the possibility that much of our science is idiographic, was widely felt and noted independently of this classification (see, e.g., Cohen 1971). Mayr (1982) and especially Shrader-Frechette and McCoy (1993) contend, as I do, that the dearth of general laws does not make ecology less worthy of study than physics, for example, but dictates a rather different method of study.

Shrader-Frechette and McCoy (1993) argue that because communities are idiosyncratic, elucidating their structure and workings should be aimed not at deducing general laws but rather at amassing a catalog of case studies. These case studies serve two main purposes. Individually, they can help to solve specific environmental problems. The first National Research Council report on using ecology to solve environmental problems (National Research Council 1986) provided several case study examples in this vein. Second, as a group, case studies can point to rough generalizations that can guide and facilitate further case studies; in other words, they advance both theory and

practice. Lawton (2000, p. 15) concedes that “there is now a suite of wonderful, individual studies in this genre, and I am not convinced that we need many more.” I disagree; the fraction of community types that have been studied adequately in this vein is quite small, and there are not nearly enough such studies.

According to Pickett et al. (1994, p. 26), “understanding is the overarching goal of any science” (cf. Ruse 1988). Any science that achieves such understanding has epistemic value. For most sciences, “understanding” means understanding how nature works, that is, being able to answer questions about a natural phenomenon by referring to certain patterns, relationships among entities and processes, and causes of the patterns and their differences (Pickett et al. 1994). Generalization is not the only tool for achieving basic scientific understanding. In community ecology, general laws might even mask understanding of mechanisms (Chave et al. 2002). Other important tools for achieving understanding are causal explanation and testing. Although the concept of cause has several layers of meaning (Kuhn 1977), a causal explanation is the determination of the conditions, processes, and mechanisms that yield a pattern or phenomenon (Pickett et al. 1994). Community ecology is rife with examples of causal explanation, and the fact that almost all are quite local does not mean they are not major scientific achievements. The typical contingency noted above dictates that most causal explanations in ecology will entail substantial understanding of conditions, so perforce will be local. Testing, that is, examination of a pattern or causal explanation to assess its validity and domain, is not only a normal feature of good community ecology but also, because of the overarching contingency, will automatically reject most proposed generalizations. Again, the nature of communities ensures this result; it does not mean that the community level is unworthy of study or that the understanding community ecology achieves is weak or deficient.

To me, then, Lawton’s unease and pessimism about the status of community ecology seem like another version of misplaced “physics envy” (Cohen 1971). It is misplaced on at least two counts. First, the laws of physics are all *ceteris paribus* laws, formulated with all other forces, etc., assumed minimal, and the actual governance of, for example, particle movement in any particular instance is much more complicated than these general laws would imply (Cartwright 1983). Second, communities cannot and should not be studied the way physics is studied; the nature of the beast demands different approaches.

So I agree with Lawton that community ecology has few interesting and useful general laws, but I disagree with him that this dearth somehow represents a failure of community ecology or indicates that community ecology is inherently weak and not worth pursuing. And I strongly

disagree with his prescription: a retreat to the study of single-species populations combined with moving on to macroecology, which entails sacrificing local detail to study patterns at continental or global scales (Brown 1995).

Many of the best community ecological case studies are both local and heavily experimental, as exemplified by classic research on the impact of carnivores on local diversity of their prey (e.g., Paine 1966) or on keystone species generally (e.g., Brown 1998). Lawton (1999, 2000) does not see a promising future in this approach and concedes only that whole lake manipulations (e.g., Carpenter and Kitchell 1993) have allowed the elaboration of some relatively simple, though contingent, rules. He attributes this success to the fact that the aquatic component of lake communities consists of relatively few key species and rather simple food web topology, traits not characteristic of most communities. However, I would argue that one of the major triumphs of community ecology is precisely the plethora of local experiments that demonstrated both the fact that community ecological rules are contingent and the nature of that contingency. In addition, this sort of experimentation has been crucial to another key conceptual advance of ecology. The growing number of experiments in nature, generally on local communities, helped foster the realization in the 1970s that ecological patterns do not alone imply a specific process (Wiens 1973, 1984) and led to an increased focus on actual mechanisms. In this sense, Lawton's prescription to move on to macroecology would be a step backward.

Similarly, a return to population ecology would constitute a real retreat. Of course, our understanding of population dynamics and distributions has advanced enormously during the same period that traditional community ecology has developed firmer conceptual underpinnings and a growing catalog of case studies. However, to move beyond phenomenological description to understand population dynamics and distributions in nature requires community ecological research at some level. The examples I provide all entail traditional community ecology, but each also incorporates remarkably insightful research on particular populations within communities. A main thread of ecological research since the 1960s has been the recognition that component species differ enormously in their importance to their communities by virtue of their activities or biomass. Community ecological research has naturally evolved to focus on how these species—be they keystones (Paine 1966), foundations (Dayton 1972), transformers (Wells et al. 1986), engineers (Jones et al. 1994), or simply dominants—interact with the rest of the community. However, this work is primarily local, reductionist, and experimental, the features that typify traditional community ecology for Lawton (2000).

The contention that biodiversity per se affects ecosystem

functioning is a search for a useful generalization about communities that rests squarely on local species richness. Although the results of this research program to date are controversial (Naeem 2003; Wardle and Grime 2003), its practitioners view it as “an exciting, important, and rapidly developing field” (Mooney 2002, p. 17), and a recent monograph (Loreau et al. 2002) describes a vigorous research effort engaging many ecologists, including John Lawton (e.g., Naeem et al. 1999), in both empirical and theoretical research along these lines. With respect to the scale of study, it is important to note that this research generally addresses only community biodiversity and functioning of local ecosystems.

Community Ecology and Environmental Problem Solving

My disagreement with Lawton's prescription stems partly from my belief that most of the societal problems ecologists are called on to help solve are fundamentally about communities, and we cannot solve them without the continuing pursuit and advancement of ecology at various scales, including traditional community ecology. I concede that the few generalizations about community ecology are not very useful in guiding management. As Levins (1966) pointed out, in order to understand, predict, and modify (manage) nature, we would like our models to maximize generality, realism, and precision simultaneously, but this is impossible. One strategy is to sacrifice realism to generality and precision. I am arguing that in most specific ecological management situations, general ecological laws are simply not realistic enough to be useful.

However, I reject the consensus claimed by Hansson (2003) that ecology has failed to provide solutions to environmental problems. Traditional community ecological studies of local communities are often highly effective in understanding environmental problems, and though political, social, and economic interests may interfere with ecologically based recommendations, community ecology also has an impressive record in guiding management to deal with such problems. To buttress this contention, I will point to examples from two related aspects of conservation biology: managing threatened species and communities and managing invasive introduced species. Lawton (1999, p. 182) is skeptical that traditional community ecology can help deal with management issues: “I doubt we could ever build a useful, practical model of an assemblage of even ten or twenty species (never mind hundreds of species) for management purposes.” On the contrary, I believe traditional community ecological research is uniquely able to help identify the small group of species among the 10, 20, or hundreds that are crucial to com-

munity structure and function and to guide management of them.

Threatened Species and Communities

The red-cockaded woodpecker (*Picoides borealis*) was one of the first species listed under the Endangered Species Act and has been a persistent source of conflict among the forest industry, the federal government, and conservationists. Historically, its decline has been ascribed to changing land use leading to loss of mature longleaf pine (*Pinus palustris*) forests on private land in the southeastern United States (U.S. Fish and Wildlife Service [USFWS] 1979, 1985, 2003). As numbers dwindled and woodpeckers came to be concentrated on public (especially federal) land, the continuing decline was attributed to hardwood midstory encroachment that caused abandonment of cavities, loss of old trees, forest fragmentation, and difficulties in finding mates in isolated populations (James et al. 1997; Conner et al. 2001). Consideration of these factors has led to a recovery plan (USFWS 2003) that emphasizes such species-specific engineering tactics as an enhanced program of moving individual birds and installing artificial cavities combined with more frequent burning and provision of an increased number of old trees. The U.S. Fish and Wildlife Service (2003) confidently expects delisting by 2075, but signs are not all encouraging. The species continues to decline on private and state lands, though populations have at least stabilized on intensively managed federal lands. Although the longleaf forest is species rich (e.g., there are several hundred native groundcover plants [Walker 1993; S. Hermann, personal communication]), the federal effort has been heavily focused solely on the woodpecker and the pine.

Frances James and her colleagues (James et al. 1997, 2001), intensively studying the woodpecker and its direct and indirect interactions with a number of other species in the Apalachicola National Forest in Florida, have discovered a wealth of information that suggests management will not be so simple and will have to account for various factors not considered so far. The woodpecker diet consists primarily of the arboreal ant *Crematogaster ashmeadi* (Hess and James 1998). In this particular forest dominated by longleaf pine, *C. ashmeadi* colonies (each exclusively occupying one [usually] or more trees) inhabit galleries abandoned by bark-mining caterpillars, especially those of a cossid moth (*Givira francesca*), as well as twigs hollowed by wood-boring beetles and termite galleries in ground-level bark (Tschinkel 2002). The ants do not excavate their own cavities and thus depend on other insects. Newly mated *C. ashmeadi* queens seek out twigs hollowed by buprestid or cerambycid beetles on pine saplings, so trees acquire their colonies early, and growing colonies move

into other chambers (produced by moths) as these become available.

Another important fact concerns the distribution of calcium in this forest and the species inhabiting it. Calcium can limit clutch size in songbirds (see, e.g., Graveland and Van Gijzen 1994), and calcium concentration in various species in this forest varies spatially (P. F. Hendrix, R. Potter, and F. C. James, personal communication). The longleaf pine ecosystem requires frequent fire, an important process in nutrient cycling. With such burning, typical herbaceous ground cover plants are replaced by hardwoods. Calcium is sequestered by these new plants, and its concentration in both arthropods and pines falls. The diet of *C. ashmeadi* is poorly known (Tschinkel 2002) but is believed to be small arboreal arthropods. These arthropods, including herbivorous species, must transmit calcium to the ants and ultimately to the woodpecker. Thus, prescribed fires or other measures are needed to limit hardwood encroachment.

When James and her colleagues analyzed the growth and mortality rates and size structure of longleaf pine trees in this forest, they found that, even where there is a vigorous prescribed burning program limiting hardwood encroachment and an officially recovered woodpecker population, recruitment of sapling pines is insufficient to provide a sustainable forest, including an adequate supply of large old trees. Thus, in addition to whatever management will be directed at the woodpecker, there will have to be further management directly related to providing a multiaged forest (James et al. 2003).

Although many details of this woodpecker-centered system remain to be elaborated, it seems likely that some form of ecosystem management will be required to maintain all critical components of this system. The current management plan (USFWS 2003) describes itself as a mixture of single-species management and ecosystem management, but it is primarily focused on the former, referring to the woodpecker as an umbrella species, that is, one whose habitat requirements are so demanding that managing this species by managing its habitat will benefit many other species (Caro and O'Doherty 1998; Simberloff 1998). Without the sort of intensive community research (much of it in a natural historic vein and some of it rigorously experimental) conducted by James and her colleagues, several components of the forest that bear on the woodpecker would not even be recognized. Use of the woodpecker as an umbrella species to try to maintain them all in appropriate states would be at best a blunt tool and at worst would simply not work.

Another example of how detailed community study is crucial to understanding threats to communities and their component species and how to manage them comes from extensive research by Paul Dayton, Mia Tegner, James

Estes, and their colleagues on kelp forest communities of the northeast Pacific (Estes and Palmisano 1974; Dayton 1975, 1985; Tegner and Dayton 1977, 1981, 2000; Estes et al. 1978, 1989; Simenstad et al. 1978; Dayton and Tegner 1984; Dayton et al. 1992; Estes and Duggins 1995). These kelp forests are of great conservation concern because they are a dominant, species-rich, spectacular feature of some regions, harbor species of special concern (such as the sea otter [*Enhydra lutris*] and abalones [*Haliotis* spp.]), undergo drastic declines (Dayton 1985; Steneck et al. 2002), and are of great economic value.

Although increasing anthropogenic sedimentation and pollution affect kelp recruitment (Dayton et al. 1992), the main human impact on kelps has come from hunting of sea otters and large fishes, such as sheephead (*Semicossyphus pulcher*; Estes and Duggins 1995; Tegner and Dayton 2000). The near total removal of these species sometimes contributes to dramatic proliferation of sea urchins, which devastate kelp beds and create "urchin barrens." However, because some kelp forests are also intermittently devastated by natural events, such as drastic storms (Dayton 1985), teasing apart the causes of great fluctuations has been difficult and has entailed intensive field study.

One of the clearest examples of top-down regulation of an entire community is provided by the recovery of sea otters in Alaska (Estes and Palmisano 1974; Estes et al. 1978, 1989; Simenstad et al. 1978; Estes and Duggins 1995). Loss of sea otters to hunting in the eighteenth and nineteenth centuries caused massive increases in numbers of many invertebrates, including urchins. Destruction of kelps by urchins, in turn, affected many species, such as large nearshore fishes and even gulls. Domination of community productivity shifted from kelps to phytoplankton. All these features were redressed by sea otter recovery in the twentieth century. Removal of invertebrate herbivores by otters allowed competition among algal species that produced a complex but predictable spatial structure (Dayton 1975).

The interaction of kelp forests, sea urchins, and their predators also provides an excellent example of just how local community ecology is in that superficially similar systems, sharing some of the same species, may be governed in very different ways (Steneck et al. 2002). In southern California, canopy-forming kelps dominate, whereas in Alaska, they are subordinate to epibenthic kelps (Steneck et al. 2002). In southern California, sea otter numbers were probably so reduced even by native Americans that they have long been an unimportant factor in the urchin-kelp interaction (Dayton 1985), but their role was taken by sheephead and spiny lobster (Tegner and Dayton 1981); in Alaska, there was no such array of alternate predators (Steneck et al. 2002). Fishing has now greatly affected the numbers and size distributions of these predators in Cal-

ifornia (Dayton et al. 1998). Unlike in Alaska, where variation in physical conditions seems not to be a major current driver of the system, in California, large events such as El Niños and storms can cause direct mortality of kelps and also indirect mortality by removing drift algae and thus driving urchins to feed on kelps (Dayton 1985). However, even in the absence of major predators, urchin populations in southern California can be at least temporarily devastated by disease, allowing urchin barrens to recover (Dayton et al. 1992). In Alaska, urchin epizootics are not a factor, possibly because temperatures are too low (J. Estes, personal communication).

This intensive, often experimental, and fundamentally natural historic research has elucidated the details and causes of temporal and spatial variation in extent of kelp forests. It has also suggested which components of the system may require management and whether various management procedures will be effective. For example, the large program (<http://www.cacoastkeeper.org/cacoast/current-programs-kelp-restoration.html>) to seed kelp beds seems extremely unlikely to be useful because the problem faced by the kelps is not germination and early growth but rather subsequent survival (Dayton et al. 1992, 1998). Conversely, intensive harvesting of all relevant urchins, at least at the scale generated by fisheries, has already been shown to be effective in at least some locations precisely because it affects kelp survival. However, in southern California, where the urchin fishery is wholly focused on red urchins (*Strongylocentrotus franciscanus*), large, unharvested purple urchin (*Strongylocentrotus purpuratus*) populations generate substantial barrens (P. Dayton and J. Estes, personal communication).

This research also provides extensive information on specific interactions that may determine the numbers and distribution of many species of these communities. For example, fishing for red urchins began in the early 1970s in California and expanded to become an enormous industry. Because juvenile abalone shelter under the spine canopy of adult red urchins (Tegner and Dayton 1981; Dayton and Tegner 1984), it is entirely possible that the urchin fishery contributed to abalone recruitment failure (Tegner and Dayton 2000). Further, the urchin barrens produced by the red urchin and the purple urchin ultimately consist of a pavement of encrusting coralline algae that induce abalone larvae to settle (Morse et al. 1980), so the urchins, though they may compete with abalone for scarce food, may aid abalone population growth when food is abundant (Tegner and Dayton 2000).

Invasive Introduced Species

Introduced species are an enormous environmental and conservation issue, the second most important threat to

native species after habitat loss (see, e.g., Wilcove et al. 1998), and they have spawned an entire new field, invasion biology. Although some aspects of invasion biology are fundamentally at the population level (e.g., epidemiological models of spread) or the regional or continental level (e.g., regional comparisons of fractions of a biota consisting of invaders), most key issues in invasion biology of both academic and applied interest fall squarely at the community level. It is increasingly recognized that whether an invader establishes and what impact it has are determined by the interaction between that species and the recipient community (Simberloff 1986; Mack et al. 2000). The two main practical questions about established invaders are whether to do anything about them and if so, what? The first question can be answered only by detailed community research, and the second may be greatly facilitated by it in particular instances.

For recent and, especially, rapidly expanding introductions, an eradication attempt by brute force is sometimes appropriate and may require little detailed population or community biological knowledge (Simberloff 2003). Particularly, if there is reason to suspect the invader will substantially affect the recipient community, to delay management until a fuller understanding of community effects is available may lead to the tragic loss of an opportunity to eliminate a potential problem at the outset, at fairly low cost and with good probability of success (Simberloff 2002*b*).

However, once an invading species is well established, a number of technologies are available to manage introduced species at acceptably low levels (Simberloff 2002*a*). Unfortunately, resources are insufficient to attempt maintenance management of every invader. Thus, the most important management question is about community ecology: How will a particular invader affect recipient communities? Answering this question often entails ingenious, detailed research on complicated systems because many impacts of introduced species are subtle even if devastating. Shea and Chesson (2002) have suggested traditional community ecology as a framework for understanding invasions and have pointed to recent advances in community ecological theory that can both help guide study of specific invasions and allow such studies to enrich community ecology. Further, if an invader is found to have a substantial enough impact that management is desirable, community ecological research often points to feasible means.

The longleaf pine-dominated communities that house the red-cockaded woodpecker may present an optimistic picture for management of introduced species. In intact stands of this community maintained by frequent, low-intensity fires, invaders that plague surrounding areas are notably absent or are in very low numbers. For example,

the red imported fire ant *Solenopsis invicta* has become a famous scourge throughout the Southeast (Tschinkel 1993). However, its greatest densities are in disturbed areas, including those naturally disturbed by flooding (Tschinkel 1993); agricultural lands and lawns are particularly heavily invaded. It is an interesting fact that in routinely burned, longleaf pine-dominated forests of the Apalachicola National Forest in Florida (McInnes 1994) and the Wade Tract in south Georgia (D. Simberloff, personal observation), areas colonized by this species in the 1950s, *S. invicta* is absent or is present in low numbers; it is largely restricted to road verges and (in the Apalachicola National Forest) pond margins. Instead, the native fire ant *Solenopsis geminata* is common in the forests. This absence or relative rarity of *S. invicta* in longleaf forests except in disturbed areas apparently characterizes the entire Southeast (Folker et al. 1993). The reason *S. invicta* does not usually persist in these forests is unknown, but the impact of this ant on communities it has penetrated has been enormous. For example, native ants are greatly reduced in numbers and species richness (Gotelli and Arnett 2000; Gibbons 2002).

Not only are imported fire ants conspicuously missing from the Wade Tract, but introduced plants are missing as well, even though approximately 40 nonindigenous plant species are found within 200 meters of the Wade Tract and many more in residential and agricultural areas within a few kilometers. The Wade Tract comprises approximately 80 hectares, is routinely burned during the growing (lightning) season (Hermann 1993), and contains almost 400 species of native plants in its ground cover (S. Hermann, personal communication). Individuals of approximately 11 introduced plant species are also present, but almost all are within 2 meters of human disturbances, particularly trails. Why introduced plants have not invaded the Wade Tract in greater numbers probably has to do with the frequent growing season fires, which destroy the invaders; the trails are the only areas that rarely burn. If an introduced species adapted to the prescribed fire regime of the Wade Tract (frequent low-intensity growing season fires mimicking the natural, lightning-driven fire regime) were to establish in this area, it might succeed, spread, and effect wholesale change at least in the ground cover community, the repository of most of the biodiversity. Asian cogon grass (*Imperata cylindrica*), well established nearby, might prove to be such an invader.

Ecosystem Management for Invasive Species and Threatened Species and Communities

The absence of substantial invasion so far in the Wade Tract suggests a novel approach to managing introduced species. Most current techniques for managing introduced

species target specific invaders (Simberloff 2002a). The main methods are various kinds of mechanical and chemical control (or combinations of these two technologies) and biological control. Although there are many success stories for all of these species-specific methods, the fact that the number of established introduced species continues to grow induces a degree of pessimism about the prospect that even a ramped-up effort along these lines will control this global problem.

Ecosystem management has attracted great attention recently as a general approach to managing natural resources (Meffe and Carroll 1994), although it is rarely discussed in relationship to management of introduced species (but see Louda 2000). It is particularly frequently cited with respect to threatened species, and the current management plan for the red-cockaded woodpecker (USFWS 2003) touts itself as partly an ecosystem management plan. In the United States, virtually all federal and many state agencies have adopted it as the operative means of natural resource management (Morrissey et al. 1994). However, it has largely been a catchphrase rather than a group of well-defined and tested techniques (Simberloff 1998). Although it is ill defined, the general notion is that an entire ecosystem, rather than individual species, should be managed to deal with some resource issue. This suggestion reflects not only the prospect of economies of scale (managing all species at once rather than each species separately) but also the recognition that, in nature, interactions among species and between them and their physical environment are simply too intricate and critical for management to ignore, except in such highly modified settings as agriculture, silviculture, aquaculture, and mariculture. There is not yet a stable, agreed-on definition of ecosystem management, even among agencies that have adopted it as a *modus operandi*, but certain features typify most definitions (Grumbine 1997; Simberloff 1998). Chief among these is managing processes, in the belief that managing certain processes will maintain all community components. Of course, fire regime is such a process, and it has been prominently featured in discussions of ecosystem management. In longleaf pine forests, a particular management tool (routine growing season fires) helps to maintain an entire ecosystem (fig. 1A). Knowing exactly what mix of fire and other management tools is needed to both maintain threatened species and repel invaders requires intensive research on local longleaf pine communities and would entail experiments. The research on this system goes a long way toward suggesting a management regime (cf. James et al. 2003). And, of course, whether some version of ecosystem management—particularly, the maintenance of some aspects of a natural disturbance regime—can keep other communities largely intact in the face of potential

invaders would require quite local similar research on those particular communities.

A kelp-urchin-predator system, this time on the Atlantic coast of North America, provides another example of how community ecological research can elucidate the impact of a group of introduced species. The green alga *Codium fragile* ssp. *tomentosoides* first invaded at Long Island around 1957 and has since spread south to North Carolina and north to Nova Scotia (Carlton and Scanlon 1985; Chapman et al. 2002; fig. 1B). Through interactions with a number of other species (primarily introduced), it has transformed formerly kelp-dominated regions. The nature and mechanisms of this transformation have been intensively studied in the Gulf of Maine (Harris and Mathieson 2000; Harris and Tyrrell 2001; Levin et al. 2002) and Nova Scotia (Chapman et al. 2002). The research is in the vein of traditional community ecology, with a substantial experimental component.

In the southwestern Gulf of Maine, a kelp forest dominated shallow water areas through the 1970s. Beginning around 1980, populations of the native green sea urchin (*Solenopsis droebachiensis*) increased greatly, converting many areas into typical urchin barrens (Harris and Mathieson 2000; Harris and Tyrrell 2001); overfishing of large fishes probably led to the urchin explosion (Harris and Tyrrell 2001). A major urchin fishery developed in the late 1980s, leading to reversion of previously barren areas to algal cover. However, rather than native kelps, *C. fragile*, which had arrived in the Gulf by 1964, dominated the new canopy in many areas (Harris and Tyrrell 2001). It is significant that urchins and other grazers do not regulate *C. fragile* (Chapman et al. 2002; J. Estes, personal communication). The spread and dominance of *C. fragile* has been facilitated by another introduced species, the bryozoan *Membranipora membranacea* (Harris and Tyrrell 2001; Levin et al. 2002), a prime example of invasional meltdown (Simberloff and Von Holle 1999) in which invaders exacerbate one another's impacts (fig. 1C). In this instance, *M. membranacea* encrusts kelp blades and causes defoliation and leads to gaps in kelp forests, thus facilitating establishment by *C. fragile*.

In particular localities in the Gulf of Maine, other introduced species (the tunicate *Diplosoma listerianum* and the red alga *Bonnemaisonia hamifera*) and opportunistic native species (the mussel *Mytilus edulis* and brown alga *Desmarestia aculeata*) play important supporting roles, and the entire complex has facilitated the invasion of still other species. However, the key players in this complex invasive juggernaut are *C. fragile* and *M. membranacea*, and the upshot is that a group of novel communities are coming to dominate large parts of the shallow regions of the Gulf of Maine (Harris and Tyrrell 2001).

On the Atlantic coast of Nova Scotia, a natural cyclic



A



B



C

Figure 1: A, Burning longleaf pine and wiregrass in Apalachicola National Forest, Florida (source: C. Hess). B, Kelp bed being overrun by *Codium* in Gulf of Maine (source: P. Levin). C, *Membranipora* overgrowing a kelp (*Laminaria*) in Isles of Shoals, New Hampshire coast (source: P. Levin).

alternation occurred between luxurious kelp forests and urchin barrens. The entire cycle may have been initiated or exacerbated by overfishing of large predatory fishes, as in the Gulf of Maine, and was driven by voracious grazing of the kelps by green sea urchins, followed by devastation of the urchin populations by an amoebic disease (Chapman et al. 2002), possibly facilitated by the increased urchin densities (J. Estes, personal communication). However, arrival of *C. fragile* and *M. membranacea* has disrupted this cycle to the extent that *C. fragile* now dominates hundreds of kilometers of coastline (Chapman et al. 2002). The bryozoan aided the destruction of the kelp canopy during an urchin proliferation, and *C. fragile* dominated the recolonization of the barren once the disease largely eliminated the urchins.

The subsequent impacts on animals and plants of these regions in which kelps have been replaced by *C. fragile* have begun to be studied in detail (see, e.g., Harris and Tyrrell 2001) and will undoubtedly be great (Chapman et al. 2002). To date, no management procedures have been suggested to redress this invasion; the main conservation response has been pleas to tighten regulations and practices that bring new invaders to coastal waters. The ability of *C. fragile* to initiate plants from floating fragments will greatly complicate control measures.

Community Ecology and Global Change

Lawton (2000) indicts traditional community ecology not only for its dearth of general laws but also for its failure to deal with what he conceives as the key societal problem facing ecologists: predicting and managing the effects of global change. Here again, the criticism is unwarranted. Four major global environmental changes are occurring nowadays—changed biogeochemical cycles (and pollution), climate change, modified land use, and biological invasions (including diseases; National Research Council 2000)—and Lawton (2000) almost wholly neglects the last one. Although it is apparent that traditional community ecology will not by itself suffice to predict impacts of these changes and find ways to mitigate them, I believe it will contribute to predicting the impacts of all of them and that it will be the main contributor to prediction of impacts of land use changes and invasions. Even for predictions of impacts of global climate change, the sorts of traditional community studies I have described are likely to be crucial. For example, Dayton et al. (1992) relate the spatial and temporal fluctuations of kelp forests and their constituent species to El Niño and La Niña events. With respect to the *Codium fragile* invasion, the pathogen that occasionally devastates the green sea urchin on the Atlantic coast of Nova Scotia cannot quite tolerate the current winter water temperature there and must periodically reinvade from

warmer waters (Chapman et al. 2002). Similarly, Harris and Tyrrell (2001) suggest that the rapid expansion of *C. fragile* in the Gulf of Maine from a few small, persistent populations at isolated sites may have been due to increased summer water temperature.

With respect to land use change and invasions, the above examples suggest that prediction of the impact will require an understanding of the workings (Lawton [2000] terms them the “rules of engagement”) of local communities, precisely because, as Lawton agrees, the rules of engagement are local. This is why I feel we need a greater catalog of good case studies. Lawton (2000, p. 49) instead feels we need more generalizations, but the examples of what he calls “useful generalizations” do not seem particularly useful to me in predicting or mitigating impacts of land use changes and invasions. Three of these generalizations relate species richness to some other feature (area, habitat complexity, and energy), while the fourth is the relationship between local and regional species richness. Even if one were to accept that generalizations exist at these levels (except perhaps for energy, a point Lawton [2000] concedes), they do not seem able to predict or guide management in any but the crudest way. For example, the most venerable of these generalizations, the species-area relationship, typically explains only about 50% of the variation in species richness (Connor and McCoy 1979); it is easy to find small sites with many species and large sites with few.

Further, the entire focus on species richness seems tangential at best to most of the real management questions. Ultimately, of course, we aim to conserve all species, but that certainly is not the goal for particular pieces of land or bodies of water. Even if it should turn out that as a statistical average, certain ecosystem functions are facilitated by increasing species richness, and thus there would be a general community ecological law justifying in functional terms the desire to conserve all species, the actual relevance of such a law to conservation may be very limited. Little effort has been expended in assessing the relative importance of biodiversity per se to ecosystem function and conservation generally (Srivastava 2002). Rather, our global goal of biodiversity conservation can be effectively served only by focusing locally on the particular species found in just a few local sites and on the few species (keystones, engineers, dominants) that structure the habitat that, in turn, largely determines which species can exist at a site. Admittedly, regional processes are important in determining impact of a global change on a local community. Lawton (2000) titles a section “We Cannot Understand Communities without Studying Larger-Scale Regional Process.” I agree, but it is equally true that we cannot understand communities without studying them directly, and I believe we cannot understand the impact

of larger-scale regional (and global) processes on them without studying them directly.

Conclusion

That traditional community ecology appears to have few if any useful generalizations does not mean it is a weak science. Aside from the inherent interest that its practitioners may derive from its pursuit, community ecological research is critically important to understanding various issues of great concern, including the impact and possible mitigation of global environmental changes. This research is often in the tradition of natural history and thus has lost some luster in academe; it is nevertheless crucial to both understanding and management (Dayton 2003; Hansson 2003). It would be especially unwise to give up on community ecology at the very time that several new tools, such as stable isotope studies and rare element analysis, show great promise of yielding new understanding. Research at levels of organization below the community (e.g., population biology) and above the community (e.g., landscape ecology and macroecology) will yield other insights, but such studies cannot substitute for community ecology. Population dynamics occur in a community context, and landscape ecology is about connections among component communities. It is not time to abandon studies of communities *per se*.

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