Biodiversity Loss and Ecological Network Structure

Jane Memmott
David Alonso
Eric L. Berlow
Andy Dobson
Jennifer A. Dunne
Ricard Solé
Joshua Weitz

1   INTRODUCTION

The world is currently experiencing exceptionally high rates of species extinctions, largely as as result of human activity (Lawton and May 1996). Currently, most conservation research on habitat destruction focuses on the species as the unit of study, looking at either the impact of habitat destruction on individual species, or collections of species from particular habitats. There is, however, increasing recognition that species and species lists are not the only, nor perhaps the best, units for study by conservation biologists. This is because species are linked to other species in a variety of critical ways, for example as predators or prey, or as pollinators or seed dispersers. Consequently, the extinction of one species can lead to secondary extinctions in complex ecological networks (Dunne et al. 2002a; Memmott et al. 2004; Solé and Montoya 2001). The presence of links between species can also lead to community closure after the loss of a species, with the result that this species cannot then be reintroduced (Lundberg et al. 2000). Moreover, in the case of restoration biology, restoration will not be sus-

tainable for a given species unless the ecological links with other species are also restored (Palmer et al. 1997).

Food webs have long been used in ecological research and provide a description of the trophic links in a community. In addition to their obvious role as descriptions of community structure, food webs are being used increasingly as the basis for an experimental approach. For example, a food web from Belize (Lewis et al. 2002) was recently use to predict the likely role of indirect effects in structuring the community, these predictions were then tested by a field manipulation (Morris et al. 2004). While food webs may be the most commonly described ecological network, other types of interaction webs are increasingly being investigated that include a variety of trophic and non-trophic interactions such as pollination, seed dispersal, interference competition, habitat or shelter provisioning, and recruitment facilitation or inhibition (e.g., Bascompte et al. 2003; Dicks et al. 2002; Jordano et al. 2003; Menge 1995). Food webs and other ecological networks have not been widely applied to the field of conservation biology, but given the practical advances being made in food web construction (for example, ecoinformatics), the theoretical advances (for example, models of extinction dynamics), and the ongoing threat of biodiversity loss, now is a good time to begin to use ecological networks as a conservation tool.

Conservation biology aims to protect intact native ecosystems and restore degraded ones. Even when these conservation goals focus on protecting one individual threatened or endangered species, there is an increasing recognition that multispecies approaches are essential for success (Chapin et al. 2000; Costanza et al. 1997; Ehrenfeld 2000; Schlapfer et al. 1999). Multispecies considerations are also critical for any ecological monitoring or assessment designed to protect key ecosystem services, such as pollution control, pest control, water filtration, and water clarity (e.g., Carpenter and Kitchell 1988). At the root of these calls for multispecies approaches to conservation and restoration is an appreciation that species *interactions* are important. Ironically, conservation, restoration, or monitoring projects rarely collect data on the structure of these interactions or how they change over time and across gradients of human impacts. In this chapter we will outline five areas of research that we believe could make a significant difference to the speed with which ecological networks can be used in conservation biology.

2   QUESTION 1: THE NATURE OF HABITAT DESTRUCTION

2.1   BACKGROUND

Habitat destruction is a collective term for a variety of environmental troubles, each of which may have different effects on food web structure and, given that they often act concomitantly, may also interact with each other in unpredictable ways. While a frequent outcome of habitat destruction is species loss, whether

the different types of habitat destruction lead to different patterns of species loss remains unknown.

2.2   WHAT IS KNOWN

Habitat destruction can be put into four main categories, none of which is mutually exclusive of the others:

a. Habitat removal leading to habitat fragmentation: This is probably the most widely known form of habitat destruction and leads to both habitat loss and habitat isolation. The hostility of the matrix between the remaining habitat fragments is likely to affect different species in different ways. For example, the rodents responsible for the spread of Lyme's disease are not affected by fragmentation whereas their competitors and predators are. This difference in matrix permeability leads to both an increase in the incidence of the rodents and in the prevalence of Lyme's disease in humans (Allan et al. 2003). This example demonstrates how food web structure can mediate unpredictable effects—here woodland fragmentation indirectly caused an increase in the prevalence of a disease affecting man. The effect of habitat fragmentation on food web structure is beginning to be addressed, for example, pioneering work by Gilbert et al. (1998) revealed that predators are both most affected by fragmentation and that they are most rescued by wildlife corridors. The experiment by Gilbert et al. (1998) combined a real (albeit micro) community with rigorous experimental design and teased apart the effects of habitat fragmentation on the different trophic levels. However, the work did not explicitly identify links between species; indeed no published work to date has replicated food webs on fragmented habitats.

b. Hunting: Hunting occurs at all trophic levels; for example canopy trees are removed from tropical rain forests in selective logging programs and vertebrate herbivores and predators are hunted as trophies and for pest control. Insects are rarely hunted, although over-collecting may contribute towards the demise of some butterfly species. Untold millions of fish, sea turtles, sharks, and manatee have been hunted from the Caribbean Ocean and today no coastal sea can be considered pristine (Jackson 2001). In addition to potentially driving the hunted species extinct, hunting will obviously also lead to the extinction of species dependent upon the hunted species, for example, host-specific species of fleas and lice (Stork and Lyal 1993).

c. The introduction of alien species: Aliens pose a significant threat to global biodiversity, second only to habitat loss (Schmitz and Simberloff 1997). They can occur at all trophic levels. Alien plants are a particularly serious threat given their ability to displace native plants, to change the composition of native plant communities, and to alter a range of ecosystem processes such as nutrient cycling and disturbance regimes. Alien herbivores constitute some of worst agricultural pests, damaging native ecosystems and costing many mil-

lions of pounds to control. Alien parasitoids, principally biocontrol agents, have been widely reported from natural habitats around the world (Boettner et al. 2000; Funasaki et al. 1988; Munro and Henderson 2002) and are the subject of considerable current concern (Pemberton and Strong 2000). Mammals are one of the most important groups of alien taxa, especially on islands (Courchamp et al. 2003). Alien insect predators can also be very common, for example in Hawaii, 38% of spiders, 23% of predatory beetles, and 14% of Neuroptera are alien species (Bishop Museum 2002). While extensive data exist on the distributions of alien species and their impacts on native species such as competitors, prey species, predators, pollinators, and parasites, and even their impact upon ecosystem properties, there is extraordinarily little data on how aliens are accommodated in food webs. In reality, only two datasets exist: Henneman and Memmott (2001) working in Hawaii and Schonrogge et al. (Schonrogge and Crawley 2000) working in the UK, both describe plant-herbivore-parasitoid networks invaded by alien insects.

How these three factors interact remains unknown. For example, if a community is fragmented, has had its top predators hunted out, and is also being invaded by aliens (a not uncommon combination of events), then do these three effects act independently or do they have a synergistic effect whereby the effect of the three together is worse than would be predicted from the effect of each individual threat? If we are to have powers of either prediction or remediation (restoration) then the data concerning the impact of habitat destruction on food webs are essential.

2.3   WHAT NEEDS TO BE KNOWN

Currently, it is not known whether food webs collapse simply in the opposite order to the way in which they were assembled or whether there is a "first in last out" (FILO) order of collapse. Essentially, these questions ask whether the restoration and recovery of ecosystem function are the mirror image of the processes that lead to decline and collapse. In essence, is there any hysteresis to ecosystem function? Here hysteresis represents the history dependence of the system; thus, if you push on something and it yields, does it spring back completely when released? If it does not, it is exhibiting hysteresis. Or are there situations in which destructive activity focuses on different trophic levels, while recovery always proceeds from the bottom up? Destructive activity varies with trophic position; thus, plants at the base of a food chain will be lost at rates slightly slower than the average; the decomposers, such as worms, soil mites and bacteria will be lost at the slowest rates. In contrast, the species that feed directly on plants will be lost at a faster rate, while the charismatic tigers and eagles that feed at the top of the food chain are lost at the fastest rate (fig. 1). An understanding of how food webs both collapse and reassemble is crucial both in expanding our understanding of how food webs are structured, and also in determining how the
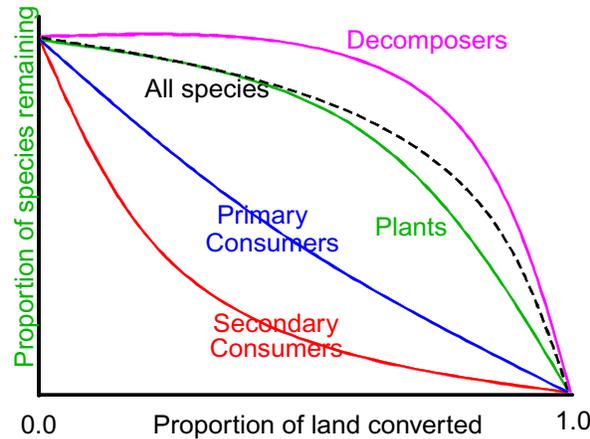
FIGURE 1   The loss of biological diversity and ecosystem services as natural habitat is eroded. The dashed line gives the classic species area decline in abundance such that a 90% loss of area dooms 50% of the original species to extinction. The lines indicate that species at different levels in the food chain will be lost at different rates.

ecosystems services they provide will decline as ecosystem functions break down due to species loss (or decline in abundance). Examples of ecosystem collapse and reassembly should provide insights into how species loss or addition leads to change in food-web structure. An important way to phrase these questions should be from the perspective of ecosystem and food web hysteresis; specifically, in which ways do the processes of food web/ecosystem assembly resemble those of food web/ecosystem collapse?

The classic example of ecosystem collapse comes from John Terborgh's work on Lago Guri in Venezuela (Lambert et al. 2003; Terborgh et al. 2001; Terborgh et al. 1997). This lake was flooded in the late 1980s to create a huge artificial lake that would drive a huge hydroelectric dam. Flooding a forested river created a series of islands of different sizes that could be studied as their faunas and floras collapsed. Island biogeography theory predicts that larger islands should conserve a greater diversity of species, which in turn should maintain a higher proportion of ecosystem services. Terborgh's work uses island size as an adjunct for time in the process of ecosystem collapse; the smaller islands have lost more species and are thus closer to total faunal and floral "meltdown." The work illustrates that food web collapse is driven by the initial loss of species from the highest trophic levels; this in turn leads to the release from predation of herbivorous species at intermediate trophic levels. The increase in the abundance of the most competitive herbivorous species in turn selects for plants that can withstand

herbivory. In the most degraded habitats, leaf cutter ants are only the herbivores that can exploit these plants, which eventually die from defoliation. The general pattern observed here is first a shortening of the web followed by a sequential collapse.

An important contrast to Lago Guri are the studies of Krakatau in the straits between Java and Sumatra (Thornton et al. 2002; Thornton et al. 1988). The volcanic eruption in 1883 completely destroyed all life on Krakatau. However, biologists have visited and surveyed the island, and the surrounding newly emergent islands, with an almost decadal frequency; this has provided a unique set of data on how island communities reassemble themselves. While most studies have focused on these data as ways of testing the laws of island biogeography, they represent a rich source of information that could be exploited by the food web community. When the species living on Krakatau are divided among different trophic levels, we see first a rapid increase in plant species at the base of the web. Herbivorous insects are blown in on the wind, followed by marine and terrestrial bird and bat species. The marine birds feed predominantly on fish, but significantly enhance the soluble nutrients on the island in the guano dumps around their nesting sites. The insectivorous birds and bats feed on the herbivorous insects. Later in the sequence of arrivals are frugivorous birds and bats, which manage to exploit the fruit produced by regurgitated and defecated seeds from the migratory species passing through the islands. When the buildup of trophic diversity on Krakatau is examined, there are some hystereses like similarities to the patterns observed in Lago Guri. There is an initial rapid assemblage of weakly interacting plant and animal species (to about 1920) followed by a slower and more steady increase in diversity at all trophic levels as interactions between species multiply, and intra- and interspecific regulation begin to replace colonization and persistence as the forces structuring the community.

The Krakatau data can be used to compare potential indices of ecosystem resilience and stability. The most widely used index is mean trophic position; this index is calculated by categorizing each species in a trophic level (e.g., plants—level 1; herbivores, level 2, etc.) and then calculating the mean for all the species in the community or food web. The index is most widely used in studies of overexploitation of fisheries, where the mean trophic level of species removed from the fishery is estimated (Pauly et al. 1998). Almost by definition, this will exclude many species from lower trophic levels from the calculation, as few fisheries actively exploit plankton. A logical extension of this calculation is to calculate the variance, or the standard deviation of trophic position. When we undertake this for the Krakatau data we find that the standard deviation provides a more sensitive index of food web change than mean trophic level. In particular, it is intriguing that mean trophic level quickly equilibrates as the Krakatau community assembles, while the standard deviation takes longer to stabilize and then does so once the different trophic levels seem to grow at roughly equal rates. Similar patterns are observed when this approach is applied to the Lago Guri data for community meltdown (Dobson unpublished). In both cases, community

change is most rapid when the standard deviation of mean trophic position falls below unity. It would be an interesting exercise to calculate the standard deviation of mean trophic level for other food webs, particularly those that are collapsing. It is probable that food webs with standard deviations of mean trophic level that fall below unity are in the process of collapse.

3   QUESTION 2: HOW DO SPECIES INTERACTIONS MEDIATE SPECIES EXTINCTIONS?

3.1   BACKGROUND

With most, if not all ecosystems facing mild to extreme stress due to a variety of anthropogenic factors, the question of whether species interactions amplify or ameliorate such perturbations takes on practical importance. Increasingly, conservation biologists and ecologists are called on to help set priorities for conservation and restoration programs. Understanding and predicting ecosystem robustness to perturbations should be a fundamental part of making sustainable conservation decisions. Food webs and other types of ecological networks can provide a very useful framework for beginning to evaluate the robustness of ecosystems to species loss, and the tendency of complex species interactions to mediate ecosystem responses. By robustness, we refer to a type of stability that focuses on the persistence of features of interest in a system in response to perturbations, particularly those not normally experienced by the system in its development or history (Jen 2003). Thus, robustness is a useful way to think about ecosystem response to perturbations such as species loss.

This section discusses a particular aspect of robustness: how differences in ecological network structure may mediate the degree to which primary species losses, however they are caused, may be followed by additional secondary extinctions. In a conservation setting, this type of research can help focus effective protection or intervention on less robust habitats, taxa, and ecological processes. This can help direct policy efforts and increased resources towards more fragile systems whose persistence may be relatively more threatened.

3.2   WHAT IS KNOWN

Food webs provide a useful framework for beginning to assess the potential robustness of multispecies assemblages to biodiversity loss, as well as the impact of losing species with different functional or structural roles within ecological networks. One recent approach for assessing ecosystem robustness uses empirical data from ecological networks and makes use of simulation techniques from network structure analysis (e.g., Albert et al. 2000). As shown in several well-resolved food webs (Solé and Montoya 2001) and pollination webs (Memmott et al. 2004), secondary extinctions are much greater when species with many linkages to other species go extinct, compared to random loss of species. These

studies suggest that regardless of the ecosystem, the order of species loss and the pattern of linkages among species strongly influence the rate of secondary extinctions. From a topological perspective, increased connectance (links per species^2) across food webs buffers the impact of species losses: As connectance increases, the robustness of food webs also increases, because, on average, species have more potential prey items (Dunne et al. 2002b).

These types of analyses also need to be done with models that include dynamics among interacting taxa. Results based on network structure may differ from what is seen in a dynamical framework. For example, a 20-species Lotka-Volterra dynamical food web has been used to study random versus ordered species losses in model systems (Ives and Cardinale 2004). By assigning species a "tolerance" to a theoretical stressor (e.g., climate change, but it could as easily represent sensitivity to habitat fragmentation or to pollutants) and then removing species randomly versus based on their level of intolerance to the stressor, it was found that the average tolerance of remaining species is greater under ordered removals versus random removals. Thus, robustness (what the authors call resistance) of the system to future change was greater under ordered loss of species. As with the previous network structure studies, the authors found that the order of species loss, given how species interact with each other as well as their tolerance to a perturbation, is very important for understanding secondary effects. Similarly, the order of species loss was found to have a profound effect on the extinction dynamics of two large plant-pollinator communities (Memmott et al. 2004). Risk is not equal for all species, but instead will be greater for species of high trophic position, rare species, and specialists (e.g., Gilbert et al. 1998). Pollinators are considered to be at higher risk of anthropogenic extinction than plants, due to their higher trophic position and other aspects of their biology (e.g., Kearns et al. 1998; Kevan and Baker 1983). By assigning pollinators a higher risk of extinction in their models, Memmott et al. (2004) ameliorated the collapse of the network.

Perhaps even more importantly, some authors also suggest that because the food web structure and dynamics change with each extinction, whether random or ordered, there is an unpredictability to compensatory dynamics that can change the potential impact of the future loss of a particular species (Ives and Cardinale 2003). In their view, this unpredictability "argues for 'whole-ecosystem' approaches to biodiversity conservation, as seemingly insignificant species may become important after other species go extinct" (Ives and Cardinale 2004). This result is consonant with a finding from a previously described network structure analysis (Dunne et al. 2002b). Dunne and colleagues showed that while ordered removals of the least-connected species often lead to few secondary extinctions, in about a third of the webs examined such ordered removals resulted in relatively high secondary extinctions. Unlike robustness of webs to loss of either most-connected or random species, which is positively correlated with connectance, robustness of food webs to loss of least-connected species is not correlated with any obvious network structure metric (i.e., species richness,

Santa Fe Institute.   July 21, 2005   3:20 p.m.   Ch14-Memmott   page 333

Jane Memmott et al.   333

connectance, omnivory). Thus, the loss of apparently topologically insignificant species could lead to large negative effects, in a way not obviously predictable from the overall structure of the food webs.

Other models of food-web dynamics that go beyond equilibrium Lotka-Volterra-type dynamics to include more ecologically plausible assumptions about nonlinear, non-equilibrium dynamics, network structure and diversity, and include ecological and evolutionary adaptive dynamics (e.g., Brose et al. 2004; Drossel et al. 2001; Kondoh 2003; Williams and Martinez 2004) will also be useful for exploring issues concerning the robustness of ecosystems to perturbations such as species loss due to habitat loss or climate change. The major challenge will be to bridge the gap between model and empirical ecosystems (whether from lab or field) to usefully predict robustness of ecosystems to different types of perturbation and species loss.

3.3   WHAT NEEDS TO BE KNOWN

Several interrelated research questions emerge out of the broad question of the robustness of multispecies assemblages:

a. Do food webs from different habitat types (e.g., terrestrial vs. aquatic, desert vs. rain forest, fresh-water vs. estuarine vs. marine, boreal vs. equatorial, aboveground vs. belowground) respond to perturbations in predictably different ways?

b. How robust are food webs to different types of perturbation (e.g., habitat damage, loss and fragmentation; species loss/removal and invasion; chemical and climatic stresses)?

c. How robust are food webs to varying perturbation intensity or order? To multiple perturbations? Are impacts likely to be synergistic? Are there thresholds of response?

d. Ecological robustness can be assessed in many different ways (e.g., persistence of species diversity, retention of ecosystem function, low probability of destructive invasions, etc.). Do different types of robustness preclude each other in the form of tradeoffs, or are they complementary?

e. Ecological robustness can be assessed for different organizational levels and ways of grouping taxa (e.g., particular populations vs. a small set of interacting populations vs. a single trophic level vs. a food web for a particular habitat vs. a mosaic of dynamically shifting habitat types with loosely linked food webs). How do particular types of robustness, or the lack thereof, at different levels relate to each other?

f. Are there general characteristics of the network structure, diversity, or dynamics of ecological networks that that can be used to predict robustness to perturbations, or can be used to suggest ways to preserve or increase desired types of robustness?

Research that touches on some of these issues for diverse, multitrophic-level systems is just beginning, and there is much more work to be done. Most of the largely theoretical work concerning complexity-stability in food webs, and the experimental and observational work concerning diversity-ecosystem function (see both briefly reviewed in McCann 2000) helps identify the potential robustness of ecosystems to perturbations. However, both of these research approaches tend to focus on more narrow definitions of internal system stability rather than on system responses to external perturbations. Each approach also lacks the combination of empiricism (characteristic of diversity-ecosystem function research) and multitrophic-level inclusion (characteristic of complexity-stability research) that is necessary to facilitate advances that may help conserve natural systems and answer the robustness research questions posed previously. An example of how the two aspects can be fruitfully combined is research that used a theoretical (but plausible) bioenergetic food-web model, parametrized with data from a 29-taxa version of the Benguela marine food web, to look at the likely impact that culling fur seals would have on fisheries in that system (Yodzis 1998, 2000). We have highlighted another approach that integrates empirical data on ecological network structure with simulations of species loss to assess ecosystem robustness (Solé and Montoya 2001; Dunne et al. 2002b; Memmott et al. 2004). This type of research has been made possible by the fact that over the last decade, more detailed data for food webs and other types of ecological networks have become available, as well as by increased computing power. Wider deployment of methods discussed at the end of this chapter will facilitate rapid compilation of future data. Improved data, combined with better analysis and modeling methods, can support crucial new research on the robustness of ecosystems to a variety of perturbations.

4   QUESTION 3: MINIMUM VIABLE AREAS FOR FOOD WEBS

4.1   BACKGROUND

Ecology has contributed two basic insights into the biology of extinction: larger areas hold more species than smaller areas and larger populations persist longer than smaller ones (Bond 1994). One key observation from field studies concerns the impact of the removal of top predators (and large mammals in general) in unleashing top-down effects. The loss of such species can promote subsequent loss of further species and eventually lead to a so-called "ecological meltdown." Such a phenomenon has been reported from predator-free forest fragments. The loss of predators generates strong imbalances shown by the disproportionate increase in the densities of prey and severe reductions of seedlings and saplings of canopy trees (Terborgh et al. 2001). An important issue here is that when looking at the space available for a given predator species, it is often assumed that it is the whole space that counts, while actually the (average) space occupied by its prey is what counts. In this context, models reveal that the fragmentation thresholds

experienced by a given species depending on a given resource are lower than one would expect by just considering the effective spatial area available (Bascompte and Solé 1998). In other words, the patchiness defined by the spatial distribution of the resource strongly constrains the metapopulation dynamics of those species exploiting it and thus their effective fragmentation thresholds.

4.2 WHAT IS KNOWN

The relevance of topology in enhancing the effects of habitat loss and fragmentation can be observed by modeling different types of community structure. Melian and Bascompte (2002) have studied small food webs involving different types of architectures. They considered four trophic web modules: simple food chain, omnivory, apparent competition, and intraguild predation. Each module contained three trophic levels with three or four species. Again, it was shown that extinction thresholds are not only determined by life history traits, competitive-colonization abilities, and landscape properties, but also by the complexity of the food web. In particular, omnivory was shown to confer the higher persistence to the top species, while interactions between the two intermediate species decrease its patch occupancy.

Beyond the few-species model, other approaches have been taken using a number of community structures with different internal organizations, for example hierarchical communities of competitors at one extreme (Stone 1995; Tilman et al. 1994) and neutral and quasi-neutral communities on the other (Solé et al. 2002). These have shown that community organization is relevant in determining the effects of habitat loss and its spatial patterning.

4.3 WHAT NEEDS TO BE KNOWN

Future research should address these topics by considering the food web structure and, in particular, should use approaches that seem to capture the fundamental traits of community organization. One particularly difficult problem here deals with the possibility of considering all kinds of community interactions (not just trophic links). How parasites and mutualistic interactions might modify previous predictions or alter the final outcome of ecosystem melting is largely unknown. Finally, when dealing with the sixth extinction at its largest scale, it is also important to provide useful tools for conservation efforts that deal with multiple scales and also include the intrinsic variability of climate and resources as an input (something largely ignored in current models of habitat destruction).

5   QUESTION 4: INTEGRATING HABITAT DESTRUCTION INTO FOOD WEB THEORY

5.1   BACKGROUND

In the past few years there has been a revival of interest in the theoretical analysis of food webs, motivated in part by advances in the theory of networks (Albert and Barabasi 2002; Strogatz 2001). While a comprehensive food web theory or theories is still very much in development, as illustrated in other chapters of this book, progress has been made in developing models that describe the static, statistical properties of food webs. The most successful of these theories is the niche model (Williams and Martinez 2000), which assumes that predation occurs in an approximately hierarchical fashion. Despite producing artificial webs in extraordinarily good accord with analysis of the largest available food webs, the niche model is not a panacea. The niche model does not purport to be a dynamic model, nor, despite the temptation, is it possible to equate niche value with a clearly measurable organismal trait such as body size. Further, there is no mechanism for maintenance of any particular food web pattern, either ecologically or over evolutionary time scales. All of these issues would be interesting courses for further theoretical investigation.

5.2   WHAT IS KNOWN

A standard approach to the study of food webs is the development of dynamical models describing changes in population densities in multitrophic systems (Drossel et al. 2001; Montoya and Solé 2003). A similar and seemingly worthwhile variation would be to develop individual-based models in which the food web and its organization constitute "emergent" phenomena resulting from competitive, predatory, and/or mutualistic spatially explicit interactions. All of these models may be viewed, with some historical deference, as the next generation of food web models based on Lotka-Volterra-type interactions (Cohen et al. 1990; Pimm and Lawton 1977; Post and Pimm 1983). The theoretical motivation for dynamic modeling is clear; food webs evolve on a variety of time scales, from the loss or introduction of a few species due to exogenous/endogenous causes, to wide-scale displacement of organisms because of climactic changes and/or anthropogenic disturbance. Only a dynamic, spatially explicit model can hope to explain the underlying ecological reasons for the observed patterns. Indeed, habitat degradation is occurring at unprecedented rates; therefore, it seems irresponsible, even reckless, to wait the necessary time to agree on a comprehensive food web theory. While progress is made on general principles underlying a dynamic, spatially explicit, and possibly stochastic food web theory, modeling should attempt to offer practical recommendations and partial answers to the crucial questions in conservation and restoration ecology. As such, we outline below what we believe

to be the most promising avenues for integrating reasonable notions of habitat degradation, an inherently spatial phenomenon, into food web models.

5.3   WHAT NEEDS TO BE KNOWN

a. Non-random destruction of habitat: Complex ecological networks such as food webs arise from explicitly spatial and often heterogeneous interactions (Holt 2002). The degradation of habitat is heterogeneous in its spatial distribution. Theoretical models of habitat destruction rarely incorporate such complexities, relying instead on simplified notions of disturbance amenable to computational and mathematical analysis. Some examples of theoretical approximations of disturbance include homogeneous site loss (Neuhauser 1998; Tilman 1994), homogeneous barriers (Nakagiri and Tanaka 2004), as well as spatially correlated degradation in models with exogenous and endogenous heterogeneity (Bolker 2003). Spatially realistic models of degradation in community/regional level food web models would be well served by borrowing from the field of metapopulation biology, in which habitat fragmentation is the norm and the methodology to deal with it has developed in kind. Examples of useful concepts include the use of incidence functions to describe the flux of immigrants between disconnected patches as well as the scaling of extinction probability with patch area (Hanski 1994). The development of inexpensive and web-available remote sensing landscape data also bodes well for opportunities to integrate explicit land-use changes, habitat fragmentation, and vegetation changes into spatial models. This is relatively uncharted territory for theory and seems to require close affiliation between theory and empiricists working on local conservation and/or ecological studies. Finally, it is worth noting that not all habitat destruction is damaging. The pitch pines of the Pine Barrens are infamous for relying on forest fires to gain an advantage over other species that have diminished ability to re-sprout and recover after fires. Taking a broader perspective, there is also evidence that at intermediate levels of disturbance the benefits of spatially limited refuges outweigh the costs to the community as a whole (Bolker 2003; Weitz and Rothman 2003). In a sense, fragmentation can lead to a spectrum of solutions to the colonization/competition tradeoff, but in a completely connected world the best competitor wins. Deciding what degree of degradation a food web can sustain without collapsing is an important problem that theory is only beginning to confront (Melian and Bascompte 2002).

b. Species-area and link-area laws: Food webs are typically defined at a fixed scale, but the composition of local communities is determined by local as well as regional processes taking place at multiple scales. There is a widely held, though controversial, belief that local interactions and regional co-occurrence are responsible for the purported power-law scaling of species richness S with area A, $S = cA^z$ (Connor and McCoy 1979; Crawley and Harral 2001; Hubbell 2001). A recent theory proposes a means to extend the species-area law to

a link-area law (Brose et al. 2004), that is, a higher-order indicator of the organization of communities across scales. This theory generates many new questions for research. For example, to what extent will such a link-area law hold in a fragmented habitat? Available empirical data might permit computational removal experiments so as to examine the robustness of the link-area laws to artificial destruction of habitat. Also, is it possible to integrate the niche model into link-area laws, or at least to parametrize the niche model and test its predictions with this scaling theory?

c. Theory for reserves: The flip side of developing theory for habitat degradation is the ongoing interest in the design of reserves (Bascompte et al. 2002; Lubchenco et al. 2003; Williams et al. 2004). The basic scientific question in reserve design may be likened to that of a Lagrange optimization problem from elementary calculus, wherein a student is asked to design a rectangular enclosure capable of holding the maximum number of cattle given a fixed amount of available fence. The answer is, of course, to construct a square enclosure. Unlike this simple example, the tradeoffs in reserve design are myriad and far more complex (Williams et al. 2004) and the "value" to be maximized is often contentious and under dispute. How many reserves should be set aside? Is it better for them to be contiguous or separated? What is the minimum useful reserve size and intra-reserve distance? How should the reserves be allocated dynamically in time (Costello and Polasky 2004)? Answering any/all of these questions is not strictly a matter of judging long-term sustainability of populations that depend on life-history, dispersal functions, evolutionary changes in organismal size, as well as on multispecies interactions. Benefits to tourism, public use constraints, and industrial access must also be considered. Some reserve design models incorporate explicit population dynamics, others do not. However, as pointed out in a review by Gerber et al. (2003), marine food webs are rarely considered. Doing so would certainly add complexity to an already difficult problem. But in the long run, understanding the future of a single population requires at least some understanding of its interdependencies within the larger web.

6   QUESTION 5: WHAT DATA DO WE NEED IF THIS RESEARCH AREA IS GOING TO GROW?

6.1   BACKGROUND

Data about the structure of species interactions will be invaluable in understanding key unanswered questions about how these interactions either respond to or mediate the effects of human perturbations (e.g., Ives and Cardinale 2004). Even coarse data about known species interactions that are relatively easy to identify (e.g., feeding links, pollinator links, and habitat or nest-site provisioning) can

provide useful information about multivariate changes in community structure across environmental gradients or in response to a human impact (e.g., Brose et al. 2004; Harper-Smith et al. in review).

6.2   WHAT IS KNOWN

Biodiversity loss is a practical issue for conservation biologists and a problem for which solutions are needed in a short time frame. If food webs are to provide part of the solution, conservation biologists need a practical means of collecting food web data. Currently, putting together a food web is a time consuming (and therefore expensive) task. Insects form the vast bulk of biodiversity and most of the recent high quality and highly resolved webs have been multiyear studies (e.g., Lewis et al. 2002; Memmott et al. 1994; Muller et al. 1999; Rott and Godfray 2000). The time and resources needed for this approach are simply not available to conservation biologists working at the coalface. Bioblitz days and the Rapid Assessment Program were developed to provide a rapid, qualitative census of the biological resources of a natural area. While these represent a departure from the painstaking methods of food web construction, similar rapid techniques may need to be developed for conservation biologists who need species interaction data and who do not have the time/resources for a conventional approach.

A "quick and dirty" approach to characterizing interaction webs contrasts with the traditional structural food web approach of gathering detailed interaction data from very few (usually one) sites; for example see Williams and Martinez (2000) and Dunne et al. (2004). The more intensive and less extensive approach to compiling typical food web data is partly the result of the traditional focus by structural food web ecologists on identifying "universal" patterns of link structure across diverse ecosystems, rather than on applications for conservation. Early food web theory was criticized as being based on incomplete webs (Cohen et al. 1990; Polis 1991) and this critique led to a more exclusive priority on gathering higher quality, detailed webs that could be used to test general theory about food web structure (Cohen et al. 1993; Dunne et al. 2004). While site-specific, intensive data on food web structure are essential in this context, we propose that data on trophic links or other interactions for one community type over time, across multiple sites, or across gradients of human impacts are invaluable for comparative analyses that quantify changes in community structure and suggest mechanisms warranting more detailed empirical investigation (Schoenly and Cohen 1991; Woodward and Hildrew 2001). Data on how these interaction webs, even if incomplete, are assembled over time within a given habitat can provide key information about community resilience (e.g., Harper-Smith et al. in review; Knapp et al. 2001) and can indicate whether or not restoration is likely to be successful.

We stress that useful ecological networks are relatively easy to construct, particularly by resource agency specialists who have an intimate knowledge of the natural history of their system, provided two conditions: (1) They are explic-

itly acknowledged as works in progress, and the relative certainty of each link is clearly specified; and (2) they are used primarily for comparisons within one system over space, time, or other conditions (e.g., invaded or not). The first condition stresses the heuristic value of the process by considering each web to be an operating hypothesis that helps target further empirical or theoretical investigations. The latter condition facilitates comparisons by minimizing variation among webs due to link uncertainties or investigator biases such as inconsistent levels of resolution within a web (e.g., top predators identified to species level and all phytoplankton lumped into one group).

6.3   WHAT NEEDS TO BE KNOWN

New "ecoinformatic" technologies for mining, managing, and analyzing data will greatly facilitate the development of extensive ecological network databases that are relevant to conservation. Many conservation sites or large-scale monitoring projects have, or will have, extensive species lists stored in spatial mapping databases. Examples include: (1) Sierra Nevada Forest Plan for bioregional monitoring (Powell and Blackwell 2001; USFS 2001) and (2) Millennium ecosystem assessment (www.millenniumassessment.org). For each species, attributes could be added that include its potential prey and predators from among the master species list, as well as species with which it is known to strongly interact in other ways (e.g., other species that provide critical nesting or nursery habitat). Then for any specified location, a *potential* network of interactions could be derived from this "meta-matrix" of interactions using the spatial information about which species coexist, and potentially interact, in that area. Thus, any interaction webs derived from this approach (called Rapid Webs) would be based on information compiled for all species found in the larger study area rather than on observations of interactions at each particular location. An example of how a Rapid Web program would work, the case of Lower Woods, a 285-hectare ancient woodland Nature Reserve in the UK, is presented in Box 1.

While these literature-based data may be incomplete or problematic to use for testing general food web theory, the consistency in how link structure is specified across all samples would facilitate comparisons among sites and across gradients of habitat fragmentation. Selective detailed studies to quantify links at individual sites could test the validity of this "meta-matrix" approach. Any developing species interaction database should include standards for specifying levels of certainty and sources for each link, and it should be flexible to accommodate new information that becomes available. Similarly, new developments in "semantic web" technology (www.w3.org/2001/sw/) could facilitate data mining of dispersed web-based documents to compile food webs, and provide for data inference based on information from related species and systems to fill in trophic links where local data are lacking. These types of semantic web technologies for biodiversity and food-web applications are being developed by the Semantic Prototypes in Research Ecoinformatics Project (SPIRE; http://spire.umbc.edu/).

Box 1: A Rapid Web Program

    Lower Woods is a 285-hectare ancient woodland nature reserve in Gloucestershire, UK, and while a species list of 2771 species exists for the site (Martin 2004) no interaction data were available. However, to date (and this is still an ongoing project) nearly 7000 trophic interactions involving species found in this woodland are listed in the scientific literature and these, together with the species list (to determine whether both predator and prey are present), can be used to construct a food web. There are problems with the web dataset, the most obvious being that the literature is not a random sample of interactions; rather it is bias towards particular groups. For example, while there are 566 potential trophic links between the 19 mammal species and their prey species, very few links can be found between the 120 species of spider and their prey. Moreover entire groups of species are missing; for example, there are apparently no aphids, earwigs, or nematodes in the wood and only 24 species of fly! However, while there are great weaknesses in the dataset, there are also great strengths. For example, the web overall contains a number of different types of networks such as predation webs, herbivory webs, decomposition webs, and pollination webs. The web also bridges the divide between freshwater and terrestrial webs and between vertebrate and invertebrate webs. To put the web together using field techniques would take decades, cost considerable amounts of money, and would have required a team of entomologists, mammalogists, botanists, mycologists, arachnologists, herpetologists, lichenologists, and ornithologists. In comparison the literature search took three months and provided a serviceable web, albeit with (known) imperfections.

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7 CONCLUSION

The five questions posed in this chapter demonstrate that there is considerable scope for adding a food web approach to the more traditional research tools used by conservation biologists. Moreover, as illustrated by the Lower Woods food web constructed from the literature, the time/cost constraints of conventional food web construction may perhaps be avoided. There may also be scope for using less detailed webs from replicate habitats as there are statistical advantages of having a small amount of data from numerous replicate habitats versus the traditional food web approach leading to a lot of data from very few (usually one) habitat. For example, data from a small section of a web for 20 degraded prairies could be compared to similar data from 20 old prairies to determine how they differ. This approach would be statistically more viable than comparing a detailed web from a single degraded prairie with a detailed web from a single old prairie. And the time it takes to gather data on the 40 small webs may indeed be comparable to the time it takes for the 2 detailed webs.

    One question remains to be answered though—does knowing the structure of the food web actually help conservation biologists to fix it once it is damaged? For example, the impact of habitat destruction on connectance is of limited practical use to a team of conservation biologists who have five thousand dollars

to restore a patch of heathland before the end of the financial year. We obviously believe that the approach has value, and is even valuable. For example, Lyzau Forup (2003) constructed replicated plant-pollinator networks for pairs of ancient and restored British heathlands. His data will provide very practical conservation advice on choosing how to restore ancient heathlands. Thus, the standard restoration approach involves positioning restored heaths adjacent to ancient heaths in the belief that insects will move from one to the other. Lyzau Forup's networks revealed that adjacent heaths shared few species and that factors other than having an adjacent ancient heath should perhaps be given greater priority in the decision making process. Moreover, his webs allowed him to ask whether an ecosystem service, that of pollination biology, was likely to have been restored.

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Jane Memmott et al.   345

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