A call to ecologists: measuring, analyzing, and managing ecosystem services

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Humans depend on ecosystem services, yet our ecological understanding of them is quite limited. In the classic example, when New York City decided to protect the Catskill Watershed rather than build an expensive water filtration plant, planners reasoned that the protection plan would be the cheaper option, even if they underestimated the area required by half. Such reasoning reflects our inability to predict how to manage lands to provide ecosystem services of sufficient quantity and quality. Human domination of the biosphere is rapidly altering the capacity of ecosystems to provide a variety of essential services; we therefore need to develop a better understanding of their ecological underpinnings, and to integrate this knowledge into a socioeconomic context to develop better policies and plans to manage them. We present a three-part research agenda to create the knowledge base necessary to accomplish this goal.

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Human domination of the biosphere is rapidly altering the composition, structure, and function of ecosystems (Vitousek *et al.* 1997), often eroding their capacity to provide services critical to human survival (Palmer *et al.* 2004). Ecosystem services are ecological functions that sustain and improve human life (Daily 1997). A recent classification of ecosystem services divides them into four categories: provisioning services, regulating services, supporting services, and cultural services (Millenium Ecosystem Assessment 2003). Provisioning services provide goods like food, fuel, and timber. Regulating services include climate and flood control. Supporting services include pollination, population control, soil formation, and other basic ecological properties upon which biodiversity and other ecosystem functions or services depend. Cultural services provide humans with recreational, spiritual, and aesthetic values. These four types of services both support and depend on biodiversity (Figure 1), yet ecological understanding of most ecosystem services remains rudimentary, impeding progress in identifying targets for conservation and management (Balmford *et al.* 2003; Palmer *et al.* 2004; Robertson and Swinton 2005). Previous work has categorized ecosystem services, identified methods for economic valuation, mapped the supply and demand for services, assessed threats, and estimated economic values (Daily *et al.* 2000; Heal 2000; Millennium Ecosystem Assessment 2003; Turner *et al.* 2003; Biggs *et al.* 2004), but has not quantified the underlying role of biodiversity in providing these services. In contrast, studies on the role of diversity in determining ecosystem function are numerous, but often examine communities whose structures differ markedly from those providing services in real landscapes (Diaz *et al.* 2003; Symstad *et al.* 2003). Moreover, such studies have generally been restricted to a small set of ecosystem processes (Schwartz *et al.* 2000). Both of these approaches – descriptive, socioeconomic analyses of ecosystem services and experimental studies of how biodiversity affects ecosystem function – are necessary, but neither is sufficient to assess how biodiversity loss affects the current and future abilities of ecosystems to provide crucial services, or to devise appropriate management strategies (Kremen 2005). Given forecasts of global declines in provision of ecosystem services (Millenium Ecosystem Assessment 2003), it is critical to develop and implement a mechanistic research agenda and to integrate it with socioeconomic work on ecosystem services in order to devise the best management and policy tools for their conservation and sustainable use (Figure 2; Folke *et al.* 1996).

In a nutshell:

- Provision of ecosystem services by native biota is both undervalued and understudied
- To correct this, ecologists need to measure the contributions of individual ecosystem service providers, determine what affects their ability to provide services, and measure the scale over which providers and services operate
- We use this approach to describe crop pollination by wild bees and dilution of Lyme disease risk by vertebrates, showing how rapidly these two services decline with diminishing diversity
- This ambitious approach requires tremendous resources; first, ecologists must gain support from decision makers and the public

The ecology of ecosystem services

To manage ecosystem services in a changing world, we need to know how human activities affect the key species

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Figure 1. *(a) Provisioning services: in Madagascar, people living near the rainforest rely on over 35 species of wild rainforest plants simply to build their homes, and use over 100 other species for various basic necessities (Kremen* et al. *1998). (b) Supporting services: parasitoids help to control herbivorous insects (parasitized sphingid moth larva in Costa Rica). (c) Regulating services: forests surrounding rivers provide flood control and can help to justify conservation (the Namorana River in Ranomafana National Park, SE Madagascar). (d) Cultural services: the helmet vanga (*Euryceros prevostii*) is a rare, endemic species that attracts bird-watchers and tourists to Masoala National Park, Madagascar.*

or functional groups that provide these services, and the spatial and temporal scales of both disturbance and recovery. How do real-world changes in communities affect the magnitude and stability of ecosystem services? A comprehensive research program to define the "ecology of an ecosystem service" would include: (1) identifying the species or other entities that are key "ecosystem service providers" and measuring their functional contributions; (2) assessing the key environmental factors that influence the ability of these species to provide services; and (3) measuring the spatiotemporal scale over which providers and services operate (Kremen 2005). Only a few services are being investigated in such a complete manner (see Case studies section), and there are no cases in which multiple services are considered, to allow development of a systems approach (T Ricketts pers comm). A broader application of this approach will help not only in planning sustainable management of ecosystem services, but also in elucidating under what circumstances managing for ecosystem services can also provide incentives for conserving biodiversity (Balvanera *et al.* 2001), not only in protected areas, but in broader landscapes that include primarily human land use (Folke *et al.* 1996).

■ Diversity–ecosystem function

Most diversity–ecosystem function research has focused on the role of species richness in influencing function, but ecosystem functioning also depends on the identities, densities, biomasses, and interactions of populations of contributing species within a community, as well as the aggregate abundance and spatial and temporal variation of these attributes (Diaz *et al.* 2003; Symstad *et al.* 2003; Kremen 2005). The predominant experimental approach has been to construct synthetic, experimental communities that are species-poor, have artificial abundance distributions, and concentrate on several ecosystem functions within a single class of ecosystem services ("supporting services" such as plant productivity; Schwartz *et al.* 2000; Loreau *et al.* 2001). To manage ecosystem services, we

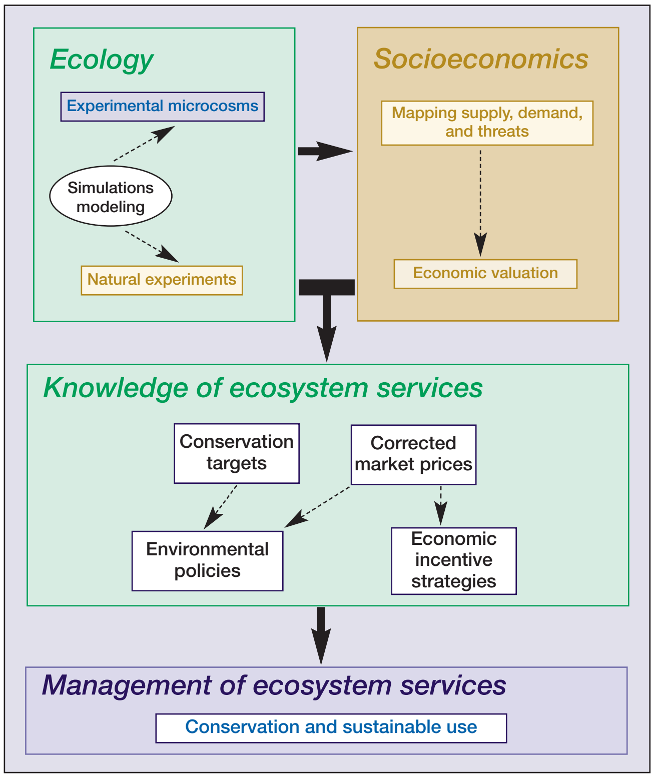

Figure 2. *Conceptual framework illustrating how greater ecological knowledge, in combination with socioeconomic knowledge, is needed to manage ecosystem services for sustainable use (Limburg and Folke 1999). Blue boxes: areas of greater current knowledge; orange boxes: poorly known (arrows indicate desired or existing linkages); white boxes: desired outcomes.*

need to understand how realistic changes in all of these aspects of community structure, acting singly or together, affect the magnitude and the stability of the ecosystem service over space and time. Ecological communities are capable of behaving in qualitatively different ways when species are lost. In some cases the provision of ecosystem services might be highly resilient, for instance if remaining species compensate for lost species, with little or no net loss in function (Schindler 1990). In others, however, species loss is accompanied by a marked loss of overall functioning (Larsen *et al.* 2005). What is responsible for these differences?

Compensation may occur through the portfolio effect (statistical averaging; Tilman *et al.* 1998); density compensation (Solan *et al.* 2004); response diversity (differential response of species to disturbance; Walker *et al.* 1999); or functional compensation (in which the efficiencies of individual ecosystem service providers change in response to changing community composition). Some studies suggest that more diverse communities are more resistant or resilient to environmental change due to such compensatory responses (Tilman *et al.* 1998; Walker *et al.* 1999). These different compensatory mechanisms may be interrelated and difficult to disentangle (Tilman *et al.* 1998) and too few studies have yet been conducted to ascertain how often each of these mechanisms operates, under what conditions, and in what types of communities. In contrast, several studies have underscored the inability of ecological communities to compensate functionally for species loss (Larsen *et al.* 2005). Determining how often and under what conditions compensatory mechanisms occur is a promising and important area for future work.

Some patterns are beginning to emerge concerning community changes that lead to rapid loss of function, although much work remains to be done. Natural communities lose species (disassemble) in non-random fashion, with some species being prone to extirpation while others are quite robust. Communities in which disassembly is non-random often lose function more rapidly than do experimental communities in which a random order of species removal is imposed (eg Petchey and Gaston 2002; Jonsson and Malmqvist 2003; Ostfeld and LoGiudice 2003; Solan *et al.* 2004; Zavaleta and Hulvey 2004; Larsen *et al.* 2005). The rapid functional loss that can accompany non-random extinction order can occur via two mechanisms. In some cases, the species that contribute the most to function are also the most sensitive to disturbance (Larsen *et al.* 2005). In other cases, non-random extinction sequences lead to the loss of entire functional groups (Petchey and Gaston 2002; Zavaleta and Hulvey 2004), eliminating the complementarity between groups that is thought to enhance function through niche differentiation (Loreau *et al.* 2001) or facilitation (Cardinale *et al.* 2003), as well as within-group redundancy, which provides insurance against species losses (Memmott *et al.* 2004).

An approach that combines observations of natural disassembly of communities in response to disturbance with targeted experiments (eg Zavaleta and Hulvey 2004) and/or simulations (eg Ostfeld and LoGiudice 2003; Larsen *et al.* 2005) will help to identify the key environmental factors affecting service provision over space and time. This information is essential for devising management plans.

■ Characterizing ecosystem services through a functional inventory

Conservation biologists recognized long ago that knowledge of species distributions provides the richest source of information for planning and managing protected area networks to conserve biodiversity (Margules and Pressey 2000). Similarly, understanding which populations, species, functional groups, guilds, food webs, or habitat types collectively produce ecosystem services (the "ecosystem service providers", or ESPs), is essential when planning for sustainable management of ecosystem services.

Two complementary methodologies exist. The "functional inventory" identifies the key ESPs in a given landscape and measures their functional contribution. The appropriate ecological level for defining an ESP is service-dependent: for example, at the genetic level for maintaining disease resistance of crops (Zhu *et al.* 2000), the population and/or food-web level for biological control of crop pests (Kruess and Tschartnke 1994; Cardinale *et al.* 2003), and the habitat level for water-flow regulation by vegetation (Guo *et al.* 2000). Researchers can then estimate the total function provided by a given community or ecosystem under different management scenarios. For example, Balvanera *et al.* (2005) estimated the annual rate of carbon sequestration in tropical forests that were conserved, regrown following conversion to pasture, or selectively logged for high value timber, based on biomass accumulation rates of individual tree species. The functional inventory permits identification of key species for management (Power *et al.* 1996); correlation of functional traits with other traits, including proneness to extinction (Larsen *et al.* 2005); assessment of the level of redundancy in the system (Memmott *et al.* 2004); analysis of interaction effects that affect function (Cardinale *et al.* 2003); and finally, prediction of the functional effects of alternative management or disturbance scenarios (Balvanera *et al.* 2005). To date, inventories of this nature have been conducted for only a few functions, including biogenic mixing of ocean sediments (Solan *et al.* 2004); water flow regulation by forest habitats (Guo *et al.* 2000); crop pollination (eg Kremen *et al.* 2002); carbon sequestration (Balvanera *et al.* 2005); disease dilution (Ostfeld *et al.* in press); and others (for examples, see Kremen 2005).

Measuring "functional attribute diversity" is a complementary approach. Here, a guild or community that provides a given service is characterized by defining the "ecological distance" that separates each ESP within it (Walker *et al.* 1999, Petchey and Gaston 2002). These ecological distances may be based on morphological, ecological, or behavioral attributes of species that are likely to result in functional differences (eg tongue length for pollinators, root depth for plants). This method is useful when it is not practical to measure the functional contribution of different ESPs for a given service. An advantage of this approach is that one can subdivide the community into groups of functionally similar (qualitatively redundant) ESPs and thus predict functional resilience with species loss (Walker *et al.* 1999) or identify guilds exhibiting functional dissimilarity (ie complementarity). A disadvantage is that the relationship between aggregate function and the contributions of each ESP is less clear. In contrast, the functional inventory method identifies how much function each ESP provides, which allows a quantitative assessment of redundancy. Using both approaches would provide the most complete (qualitative plus quantitative) and useful set of information to predict functional response to changing community composition (Kremen 2005).

■ How are we affecting our ecosystem services?

Two approaches exist for assessing how environmental factors that affect the magnitude and variability of ecosystem services vary across the landscape. Researchers could focus on the abundance of an important ESP, identified through the functional inventory, or concentrate on the function as a whole, irrespective of fluctuations in individual ESPs. The choice of approach would be informed by the results of the functional inventory. If individual ESPs are highly uneven in their functional contributions (eg dominated by a single species; Solan *et al.* 2004), an ESP-centered approach would be most useful. In contrast, if there is little quantitative or qualitative differentiation among ESPs in their functional contributions, then a function-centered approach may be best. Finally, if interactions among ESPs are thought to greatly alter function, then a function-centered approach might be more practical, although both should perhaps be used (Kremen 2005).

■ Spatial and temporal scales

Understanding the spatial and temporal scales at which ecosystem services operate will be essential for developing landscape-level conservation and land management plans. How much of a watershed's area must be maintained as forest to provide clean water for downstream communities? How should patches of natural habitat be distributed within an agricultural landscape to provide pollination and pest control services for crops, and how variable is service provision between seasons and/or years? Conversely, up to what distances might adjacent land uses affect the capacity of forest and soil ecosystems to purify water, or of natural habitat to provide pest control and pollination services? For example, Houlahan and Findlay (2004) found that land uses up to several kilometers from wetlands affect water quality, but land-use planners typically rely on narrow forest buffers of < 30 m to purify water entering rivers, streams, and wetlands. The answers to these questions about flows from ecosystem services will determine how set-asides should be distributed, and areas zoned for different land uses, in order to protect and manage the service. Because environmental effects on services may be uncorrelated across scales, studies of services should ideally be conducted at multiple, nested spatial and temporal scales (Millennium Ecosystem Assessment 2003).

■ Bringing ecosystem services into markets, environmental policies, and land-use planning

Ecological information is needed in order to design both policies and markets properly. For example, legislation under the Clean Water Act requires that wetlands destroyed by development be created elsewhere. Developers can offset wetland destruction by purchasing credits in mitigation banks consisting of restored wetlands (Bean *et al.* 1999). It is notoriously difficult, however, to replicate the functional qualities of natural wetlands through restoration (Zedler and Callaway 1999). Variation in size, shape, location, connectivity, and species composition may also substantially alter the ability of the mitigated property to replace the functions formerly supplied by the destroyed one. Thus, a unit area in

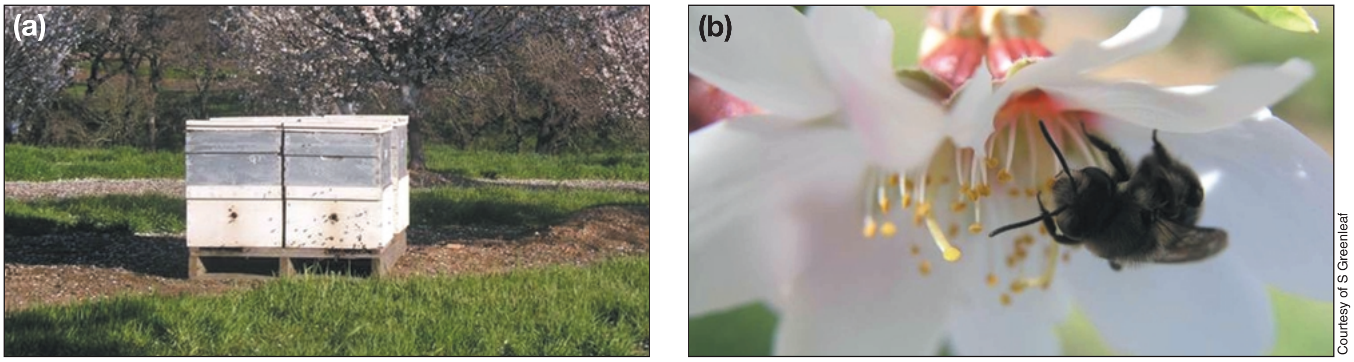

Figure 3. *(a) Honeybee boxes in an almond orchard in California, which produces 80% of the world's supply of this crop at an annual value of $1 billion. Each year, over a million colonies of honeybees are brought to California in February to pollinate almond, which cannot produce its fruit without the aide of an insect vector. Recent shortages of bee colonies have led famers to import honeybees all the way from Australia. (b) A wild, solitary bee (*Andrena cerasifolii*), pollinating almond in California, on a farm near wild habitat. Few wild bees are found on farms far from wild habitat (C Kremen unpublished).*

one mitigation bank may have a different ecological value than that in another, and ecological information should be used to govern allowed trades and influence market signals accordingly (Kremen 2005).

The use of local ecological data leads to valuations of marginal changes in services that can influence land-use decisions. For example, Guo *et al.* (2000) used ecological data to determine the relative importance of different forested habitats for water regulation in a Chinese watershed. They valued each unit of each habitat type by determining how it influenced units of water-flow regulation and hence electrical power generation at a hydroelectric plant. They then used this information to determine appropriate monetary compensation levels for landowners for not harvesting timber, based on the change in value of electrical power produced when a unit of a given habitat type was conserved rather than logged. Local-scale valuations of alternative land uses that include ecosystem services often show that the marginal benefits of conserving wild nature exceed those of land conversion and could be useful in determining best land-use practices (Kremen *et al.* 2000; Balmford *et al.* 2002; Turner *et al.* 2003). See Turner *et al.* (2003) for a review of various pitfalls in estimating economic values of ecosystem services.

Relatively few policies exist that provide incentives to protect ecosystem services. In the US, the Farm Bill now provides substantial funds for environmental conservation programs on farms and rangelands, including cost-sharing or direct payments for stewardship of soil, water, air, and wildlife habitat (www.usda.gov/farmbill/). Similar programs exist in the European Union and Australia. The Kyoto Protocol of the United Nations Framework Convention on Climate Change creates a mechanism for paying for the ecosystem service of carbon sequestration in agricultural and forest ecosystems. Even in the absence of such policies, markets for environmental services are emerging (reviewed in Landell-Mills and Porras 2002), using a variety of innovative mechanisms (Daily and Ellison 2002). Nonetheless, both policies and markets for ecosystem services are still in their infancy and much work remains to be done to make these policies effective in promoting ecosystem services, including taking a systems approach that incorporates tradeoffs between services, developing monitoring and accounting techniques, creating appropriate incentive structures, developing better land management techniques, reducing transaction costs, and finding mechanisms to encourage cooperation between private and public land managers across landscapes (Landell-Mills and Porras 2002). Each of these components would benefit greatly from a deeper understanding of the underlying ecological processes controlling provision of ecosystem services (Figure 2).

■ Case studies

We present two case studies to illustrate how this approach of documenting the relationship between biodiversity change and ecosystem function in real landscapes across space and time can contribute to policies and plans for managing ecosystem services.

Pollination services for crops in Northern California

Many farmers obtain pollination services for their crops by renting colonies of honeybees (*Apis mellifera*), whose domiciles are readily transported between farm fields. In the US, the number of managed honeybee colonies declined by 1% per year, on average, over the past 50 years (Delaplane and Mayer 2000). Large die-offs in 2004 caused by parasitic mites (up to 50% in some areas; E Mussen pers comm) have led to pollinator shortages around the country. Similar reductions in availability of this key pollinator are occurring elsewhere in the world and it is clear that our heavy reliance on this single species is a risky strategy. Many other bee species, both solitary and social, also visit and pollinate crops (Figure 3), although relatively little is known about their importance. Could wild bee populations help to reduce this reliance on honeybees, and under what circumstances?

We have quantified the contributions of wild bees in providing pollination services to watermelon, tomato, and sunflower crops in Northern California by measuring their pollination efficiencies (pollen deposited or seeds set per visit) and visitation rates (Kremen *et al.* 2002). Different but overlapping guilds of pollinators service each crop, and species contribute differentially within and between crops (eg Figure 4a). We found that wild bee communities alone (without the addition of managed honeybees) can provide partial or complete pollination services (Kremen *et al.* 2002) or enhance the services provided by honeybees through behavioral interactions (Greenleaf 2005). However, these services are rapidly eroded (Figure 4b) in response to agricultural intensification, which leads to a two-fold decline in mean richness and abundance of wild bee pollinators (Kremen *et al.* 2002). Extinction order is important; the most efficient pollinators are also the most sensitive to agricultural intensification (Larsen *et al.* 2005). In addition, density compensation does not appear to take place (Greenleaf 2005; Larsen *et al.* 2005). The proportion of wild habitat (chaparral and oak-woodland) within several kilometers of a farm is the environmental variable most strongly associated with the magnitude and stability of services, and the diversity, abundance, and productivity of foraging and nesting bees (Kremen *et al.* 2004; Greenleaf 2005; Kim *et al.* in press; Figure 5).

These findings have important economic implications. Farmers who do not have wild bees occurring naturally on their farms rent honeybees from beekeepers at considerable cost (Kremen *et al.* 2002; Figure 5). Farmers who have wild bees are partially or fully protected from sudden or gradual scarcities of honeybee colonies, whereas farmers that cannot obtain pollination services from either managed or wild pollinators may need to switch to production of crops that do not require pollination services (Southwick and Southwick Jr 1992). When pollinator shortages occur, consumers can therefore expect to pay much more for the animal-pollinated food products that constitute 15–30% of our diet (Southwick and Southwick Jr 1992).

We can use these findings, particularly the relationship between wild bee pollination services and natural habitat, to establish targets for conservation and restoration (Kremen *et al.* 2004). We have developed restoration and farm management protocols based on availability of key floral resources in natural and farmed areas of the landscape (Vaughan *et al.* 2004). We are creating spatially explicit models based on floral resource availability, bees' resource needs, and bee foraging scales, to develop alternative scenarios for managing the agro-natural landscape for pollination function. For example, could we improve pollination services equally well through landscape-scale restoration of native habitat patches off-farm, or by local-scale habitat enhancements compatible with farm management practices on-farm? Finally, we are providing this ecological information to landowners and land managers through workshops, manuals, and demonstration sites on farms.

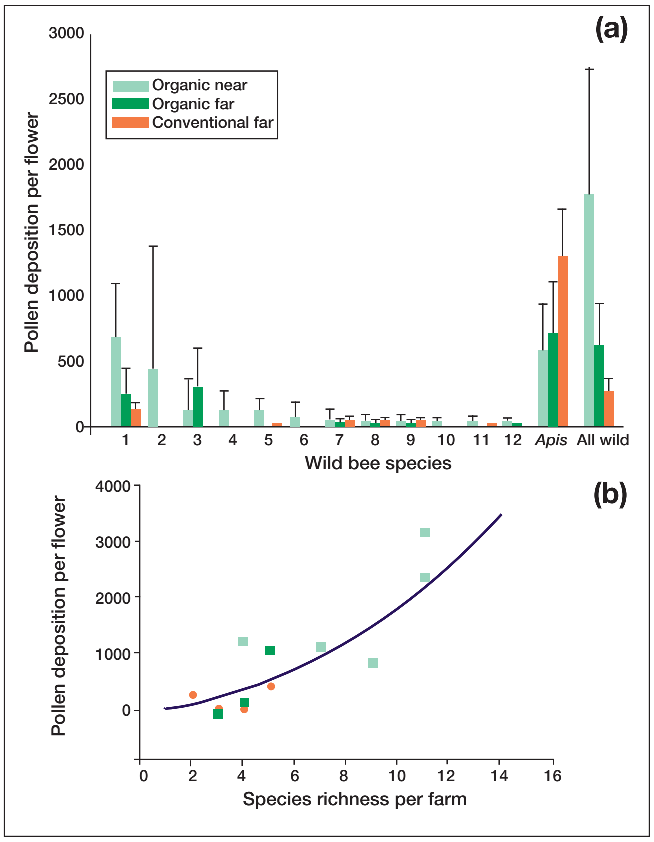

Figure 4. *Pollination services by wild bee communities to watermelon in Northern California. (a) Pollination contributions (mean pollen deposited in the lifetime of a flower, with standard error) from different species on three different farm types; farms were either conventional (using pesticides), organic (no pesticides), and far from or near to natural habitat. Each number on the x axis refers to a different species or genus of bee, ranked in order of their contributions on organic–near farms; the contribution of the honeybee (Apis) and the summed contributions of all wild bees are also shown. A flower must receive about 1000 grains of pollen to set a marketable fruit. The most important contributors either decline in abundance, and thus contribution (eg number 1), or are lost with increasing agricultural intensification (numbers 2–6). Only organic–near farms could meet all the pollination needs of watermelon from wild bee pollination alone (see Total) (adapted from Kremen* et al. *2002). (b) A power function with exponent >1 is the best fit to the relationship between pollination function and species richness on different farm sites, suggesting that pollination services erode rapidly as species are lost from the system (adapted from Larsen* et al. *2005).*

Lyme disease risk in the northeastern US

A similar framework has been applied to assess the role of vertebrate diversity in protecting humans from exposure to the most common vector-borne disease in the US, Lyme disease (LD). The causative agent of LD, the spirochete bacterium *Borrelia burgdorferi*, is transmitted

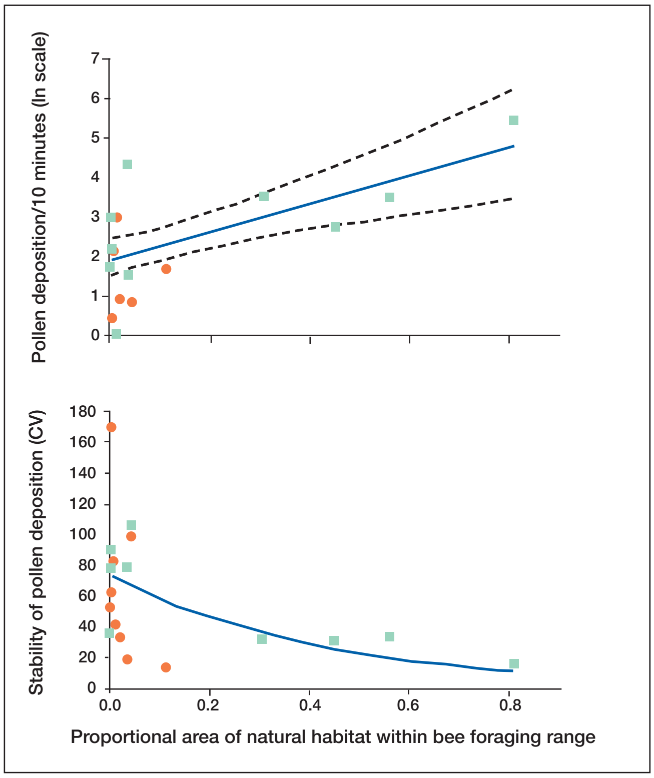

Figure 5. *Proximity to natural habitat enhances both the magnitude and stability of pollination services provided by wild bees to crops on organic (green squares) and conventional (orange circles) farms (Adapted from Kremen* et al. *2004).*

between hosts (including humans) by blood-feeding ticks (*Ixodes scapularis* in eastern and central North America). Ticks must acquire an infection during their initial (larval) blood meal in order to transmit the bacteria during the later (nymphal) meal. These ticks feed from dozens of different species of vertebrates, but the host species differ dramatically in their probability of infecting a feeding tick (Ostfeld 1997; Ostfeld and Keesing 2000).

We have quantified three host attributes that are essential in estimating species-specific roles affecting risk of human exposure to LD: (1) how many ticks an average individual of each species hosts in a given season; (2) how many host individuals occur per species per unit area; and (3) the probability that a tick feeding from a member of each host species will become infected. Together, these attributes tell us how many ticks are supported by each host species and what proportion of those ticks will become infected. Different species of mammal and bird have radically different roles influencing LD risk; white-footed mice (*Peromyscus leucopus*) infect enormous numbers of ticks, whereas most other hosts serve a protective role by acting as hosts for, but not infecting, many ticks (Figure 6a; LoGiudice *et al.* 2003).

Knowledge of species-specific roles in influencing exposure risk allows us to predict how risk will change as host community diversity declines. Computer simulations in which we removed host species in different sequences revealed how important the order of species loss is in influencing the ability of vertebrate communities to reduce disease risk to humans. Removal of species in entirely random order caused disease risk to decrease with decreasing diversity. However, the species most competent in pathogen transmission, the white-footed mouse, is highly resilient to habitat destruction and fragmentation, and even increases in abundance as habitat is fragmented and other vertebrate predators or competitors are lost (Nupp and Swihart 1996; Krohne and Hoch 1999). All simulations that incorporated the realistic scenario that mice are among the last species to be lost concluded that LD risk decreases strongly with increasing host diversity – in other words, high diversity communities perform a useful service by diluting the disease risk to humans (LoGiudice *et al.* 2003; Ostfeld *et al.* In press). Furthermore, imposition of different "rules" by which vertebrate communities disassemble under habitat destruction caused markedly different rates and patterns of increase in disease risk (Figure 6b). For example, using trophic level to determine the extinction sequence (from high to low trophic level) resulted in an initial decline in LD risk with species loss, followed by a marked increase as the final few species disappeared. Applying a sequence of species loss derived from empirical studies in fragmented landscapes of the midwestern US resulted in a pattern quite similar to the assumption that mice are always present (Figure 6b). Empirical studies confirm that LD risk, as measured by both proportion of ticks infected and numbers of infected ticks, is significantly higher in the smallest fragments that lacked diverse vertebrate communities (less than 2 ha in size; Allen *et al.* 2003). Wooded fragments of this size are typical of high-end suburbia, where it is common for people to be infected simply by spending time in their backyards. The social and economic implications of infection include diminished quality of life, school days missed, lost wages from illness, and medical insurance and treatment costs. This argues for planning landscapes to maintain larger forests with greater disease dilution capacity.

■ Conclusions

Managing for ecosystem services can have enormous scope, both for human welfare and conservation of biodiversity. For example, many major cities manage nearby forested watersheds for services (Heal 2000), and it is estimated that 13% of the terrestrial land surface could be managed for urban water use alone (Reid 2001). Now that the Kyoto Protocol has been ratified, it could potentially finance the reforestation of 3.4 million hectares per year for carbon sequestration in developing countries (Niles *et al.* 2002).

To manage ecosystem services in the future, we need to develop a better understanding of their underlying ecology, and use it to: (1) develop better market signals for ecosystem services, (2) create better economic strategies and environmental policies for their conservation and sustainable use, (3) understand tradeoffs between policies and practices that promote different services, and (4) develop management and conservation plans for services

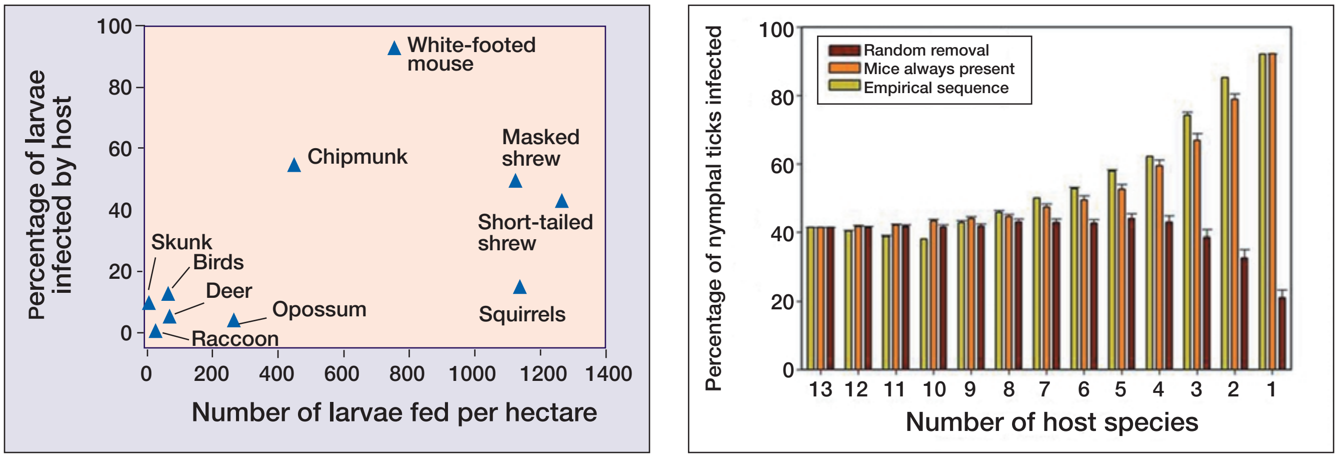

Figure 6. *(a) Position of 13 species or species-groups representing two dimensions of species-specific effects on risk of human exposure to Lyme disease. Percentage of larvae infected by each host species (ie its reservoir competence) represents the probability that a feeding (uninfected) larval tick will acquire infection with the bacterial agent of Lyme disease (*Borrelia burgdorferi*). Number of larvae fed per hectare represents the product of the average larval burden per individual member of each species and the estimated population density of that species (Modified from Ostfeld* et al. *in press.). (b) Simulations showing the consequences of three different extinction scenarios in vertebrate communities for the risk of exposure to Lyme disease, as measured by infection prevalence in nymphal ticks. In all cases, initial host communities included all 13 species or species groups. In the "random removal" scenario, species were selected for removal in random sequence. In the "mice always present" scenario, mice never went extinct (see text), and all other species were selected for extinction in random sequence. For the "empirical sequence" scenario, the order of species loss approximated that observed in fragments of decreasing size in the midwestern US (see references in LoGiudice* et al. *2003). Error bars represent standard errors from 100 simulations for each extinction scenario.*

at the whole-system level (Figure 2).

Conducting the necessary research to develop a sufficient understanding of the ecology of ecosystem services is feasible, but it may require an investment akin to that devoted to agriculture, medicine, space exploration, or defense. Ecologists will need to mount a massive awareness campaign, aimed at the public and policy makers, to convince society of the importance of ecosystem services and to demand the resources necessary to study them (Robertson and Swinton 2005). Conducting this ecological research not in isolation, but as an integrated component of teams comprising a diversity of both scientific disciplines and resource users (Biggs *et al.* 2004, Maass and Balvanera 2005) would provide a mechanism for broad dissemination of knowledge and set the stage for adaptive management (Sayer and Campbell 2004). The agenda we propose is a tall order – but nothing less than the future of humans, and that of many other creatures, is at stake.

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