

Managing ecosystem services: what do we need to know about their ecology?

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Abstract

Human domination of the biosphere has greatly altered ecosystems, often overwhelming their capacity to provide ecosystem services critical to our survival. Yet ecological understanding of ecosystem services is quite limited. Previous work maps the supply and demand for services, assesses threats to them, and estimates economic values, but does not measure the underlying role of biodiversity in providing services. In contrast, experimental studies of biodiversity–function examine communities whose structures often differ markedly from those providing services in real landscapes. A bridge is needed between these two approaches. To develop this research agenda, I discuss critical questions and key approaches in four areas: (1) identifying the important ‘ecosystem service providers’; (2) determining the various aspects of community structure that influence function in real landscapes, especially compensatory community responses that stabilize function, or non-random extinction sequences that rapidly erode it; (3) assessing key environmental factors influencing provision of services, and (4) measuring the spatio-temporal scale over which providers and services operate. I show how this research agenda can assist in developing environmental policy and natural resource management plans.

Keywords

Adaptive management, community structure, conservation planning, diversity–function, ecological economics, ecosystem function, functional structure, natural resource management, redundancy, resilience.

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INTRODUCTION

Ecosystem services are the set of ecosystem functions that are useful to humans. Many of these are critical to our survival (climate regulation, air purification, crop pollination) while others enhance it (aesthetics). Human domination of the biosphere has led to rapid alterations in the composition, structure and function of ecosystems (Vitousek *et al.* 1997) so that in many cases their capacity to provide necessary services has been either overwhelmed or eroded (Daily 1997; Palmer *et al.* 2004). There is still little detailed ecological understanding of most ecosystem services, however, impeding progress in their conservation and management (Balmford *et al.* 2003; Luck *et al.* 2003; Palmer *et al.* 2004; Robertson *et al.* 2005). When New York City decided to protect the Catskill Watershed rather than build an expensive water filtration plant, for example, it vindicated

the economic potential of ecosystem services (Heal 2000). It is remarkable, however, how little ecological information went into this decision (National Research Council 2000). Planners reasoned that even if they underestimated the area required by half, it would still be far cheaper than building the water filtration plant (Heal 2000). Numerous urban centres around the world depend on natural water purification mechanisms to provide safe drinking water for hundreds of millions of people (Reid 2001), yet we have little ability to predict how much land must be protected and how nearby land use must be restricted to provide water of sufficient quantity and quality (G. Daily & P. Jeffer, pers. comm.).

Previous work describes and categorizes ecosystem services, identifies methods for economic valuation, maps the supply and demand for services, assesses threats to them, and estimates economic values (Daily 1997; Daily

et al. 2000; Heal 2000; Millennium Ecosystem Assessment 2003; Biggs *et al.* 2004), but does not quantify the underlying role of biodiversity in providing services. In contrast, studies of biodiversity–function often examine communities whose structures differ markedly from those providing services in real landscapes (Diaz *et al.* 2003; Symstad *et al.* 2003; Larsen *et al.* 2005), and have been restricted to a small set of ecosystem processes (Schwartz *et al.* 2000). While each of these approaches have provided many valuable insights, a bridge is needed between these two approaches: one that will provide fundamental, ecological understanding of ecosystem services to assist in devising the best management and policy tools for their conservation and sustainable use. Given forecasts of global declines in basic services (Millennium Ecosystem Assessment 2003), it is critical to develop and implement this research agenda on the ecology of ecosystem services, and to integrate it within existing or future inter-disciplinary studies of ecosystem services (e.g. Biggs *et al.* 2004).

AN ECOLOGICAL RESEARCH AGENDA FOR ECOSYSTEM SERVICES

Management of ecosystem services is as complicated as managing ecosystems; past attempts to manage even single components of ecosystems such as fisheries have demonstrated the complexity and difficulty of this task (Walters & Holling 1990). We can divide the ecological component of this task into sub-topics, including: (1) identifying the species or other entities that are key ‘ecosystem service providers’ (ESPs) and characterizing their functional relationships; (2) determining the various aspects of community structure that influence function in real landscapes, especially compensatory community responses that stabilize function, or non-random extinction sequences that rapidly erode it; (3) assessing the key environmental factors influencing provision of services, and (4) measuring the spatio-temporal scale over which providers and services operate. While each of these sub-topics is a subject of active research in ecology, this approach will be most useful in influencing environmental policy and land-use planning when applied in its entirety. For maximum effect, it should also be integrated into interdisciplinary studies of ecosystem services including socio-economic aspects, but for the purposes of this paper, I will consider only the ecological component.

Carrying out such an agenda will present an enormous logistical, financial and scientific challenge, but it is not outside our human potential. We have only to look at the enormous strides made in medicine or space exploration, to name a few, to realize that is possible, given careful planning and sufficient resources.

Characterize the ecosystem service providers and their functional relationships

The services provided by ecosystems are ecosystem-wide or community attributes; nonetheless these functions can often be characterized by the component populations, species, functional groups (guilds), food webs or habitat types that collectively produce them (the ESPs). A related concept is the ‘service providing unit’, which refers to the segment of a population or populations providing services in a given area (Luck *et al.* 2003). The appropriate ecological level for defining the components is service-dependent (Table 1); for example, at the genetic level for maintaining pest, weed and disease resistance of crops (Luck *et al.* 2003), the population and/or food-web level for biological control of crop pests (Wilby & Thomas 2002), and the habitat level for water flow regulation by vegetation (Guo *et al.* 2000). Pragmatism enters in as well – although we might like to characterize the micro-organisms that cycle nutrients at the species level, the logistical impediments to doing so are huge (Nee 2004). For micro-organisms, important components of so many ecosystem services (Table 1), characterizing communities by their chemical signatures and then associating these communities with functional characteristics is a feasible approach yielding new insights (Balser *et al.* 2001; Naeem 2001). Most processes involving micro-organisms include interactions with macroscopic hetero- and autotrophs (Table 1). Understanding the interactions between microbial and macroscopic components of a given function could prove critical for managing these services.

We can characterize an ecosystem service locally by conducting a ‘functional inventory’ to identify the component ESPs and measuring or estimating the importance of each ESP’s contribution to the aggregate function. In general, the functional importance, f_{ik} , of each ESP_{*i*} in environment *k* will depend both on its effectiveness at performing the service, here termed ‘efficiency’ (e_{ik}), and its abundance (n_{ik}) (Balvanera *et al.* 2005). Both efficiencies and abundances may respond to altered abundances of resources, predators, competitors and mutualists, as well as to changing physical or biophysical parameters. It may often be impossible to determine the relationships among all of these factors; in practice, efficiencies may be measured as an ESP-specific property with a mean and variance (e.g. Larsen *et al.* 2005). Functional contributions of ESPs have been measured or estimated in this manner for disparate processes including pollination, bioturbation, dung burial, water flow regulation, carbon sequestration, leaf decomposition and disease dilution (see Table 2 for citations).

We can use functional importance (f_{ik}) to identify ESPs that are disproportionately important relative to their abundance, by looking for ESPs that rank relatively low in abundance but relatively high in functional importance, or

Table 1 Ecosystem services, classified according to the Millennium Ecosystem Assessment (2003), and their ecosystem service providers. 'Functional units' refer to the unit of study for assessing functional contributions (f_{ik}) of ecosystem service providers; spatial scale indicates the scale(s) of operation of the service. My assessment of the potential to apply this conceptual framework to the service is purposefully conservative and is based on the degree to which the contributions of individual species or communities can currently be quantified

Service	Ecosystem service providers/ trophic level	Functional units	Spatial scale	Potential to apply this conceptual framework for ecological study
Aesthetic, cultural	All biodiversity	Populations, species, communities, ecosystems	Local–global	Low
Ecosystem goods	Diverse species	Populations, species, communities, ecosystems	Local–global	Medium
UV protection	Biogeochemical cycles, micro-organisms, plants	Biogeochemical cycles, functional groups	Global	Low
Purification of air	Micro-organisms, plants	Biogeochemical cycles, populations, species, functional groups	Regional–global	Medium (plants)
Flood mitigation	Vegetation	Communities, habitats	Local–regional	Medium
Drought mitigation	Vegetation	Communities, habitats	Local–regional	Medium
Climate stability	Vegetation	Communities, habitats	Local–global	Medium
Pollination	Insects, birds, mammals	Populations, species, functional groups	Local	High
Pest control	Invertebrate parasitoids and predators and vertebrate predators	Populations, species, functional groups	Local	High
Purification of water	Vegetation, soil micro-organisms, aquatic micro-organisms, aquatic invertebrates	Populations, species, functional groups, communities, habitats	Local–regional	Medium to high*
Detoxification and decomposition of wastes	Leaf litter and soil invertebrates; soil micro-organisms; aquatic micro-organisms	Populations, species, functional groups, communities, habitats	Local–regional	Medium
Soil generation and soil fertility	Leaf litter and soil invertebrates; soil micro-organisms; nitrogen-fixing plants; plant and animal production of waste products	Populations, species, functional groups	Local	Medium
Seed dispersal	Ants, birds, mammals	Populations, species, functional groups	Local	High

*Waste-water engineers 'design' microbial communities; in turn, wastewater treatments provide ideal replicated experiments for ecological work (Graham & Smith 2004).

by finding ESPs that depart from the null expectation that relative importance equals relative abundance (Balvanera *et al.* 2005). We can assess the 'functional structure' of a community, by ranking species by their functional importance (Balvanera *et al.* 2005). The evenness of functional structure indicates whether there are only a few important ESPs, or many relatively equal ESPs. We can correlate species traits, such as body size, dispersal distance, and response to disturbance (response traits) with functional efficiency (effect traits), to characterize the suite of response and effect traits that a community exhibits and predict its resilience to disturbance (Walker *et al.* 1999; Elmqvist *et al.* 2003; Larsen *et al.* 2005).

Using functional importance values, we can predict how the aggregate function will change as the composition of

ESPs changes over space or time, along disturbance gradients, or with different management regimes. In each environment, k , the aggregate ecosystem function (F_k) is simply the sum of the contributions of each ESP_{ik} (Balvanera *et al.* 2005).

This framework for measuring functional contributions and then estimating aggregate function can incorporate much of the complexity inherent to the relationship between biodiversity and function (see below), allowing that relationship to take on the variety of functional forms that have been observed in nature (Fig. 1). It incorporates richness effects by summing over all species, identity (trait) effects by using species-specific efficiency and abundance values, and interaction effects by allowing efficiencies or abundances to vary due to inter-specific interactions or environmental context.

Table 2 Examples of efficiency measures for different ecosystem services from the literature; services are classified as regulating or supporting according to the Millennium Ecosystem Assessment (2003)

Service classification	Service	Ecosystem service provider	Efficiency measure(s)	Example (reference)*
Regulating	Carbon storage	Tree species (per capita)	Biomass accumulation rate	Balvanera <i>et al.</i> (2005)*
Regulating	Crop pollination	Bee species (per capita) or community	Pollen deposition per visit; seed or fruit set with and without bees	Kremen <i>et al.</i> (2002b)*, Klein <i>et al.</i> (2003)
Regulating	Crop pollination	Bee species (per capita)	Ratio of pollen deposition to removal	Thomson & Goodell (2001)
Regulating	Disease control	Vertebrate host species (per capita)	Disease dilution rate	Ostfeld & LoGiudice (2003)*
Regulating	Leaf litter decomposition in streams	Stream invertebrate species (per capita)	Leaf-shredding process rate	Jonsson <i>et al.</i> (2002)*†
Regulating	Pest control	Insect parasitoid species (per capita)	Parasitism rate	Kruess & Tschardt (1994)
Regulating	Dung burial	Dung beetle species (per capita)	Burial rate	Larsen <i>et al.</i> (2005)*
Regulating	Water flow regulation	Forest habitats	Water flow rate	Guo <i>et al.</i> (2000)*
Regulating	Invasion resistance	Herbaceous community (native plus naturalized species)	Invader biomass m ⁻² ; change in resident biomass/unit invader	Zavaleta & Hulvey (2004)
Supporting	Bioturbation	Benthic marine invertebrate species (per capita)	Bioturbation potential index	Solan <i>et al.</i> (2004)*
Supporting	Nutrient cycling, mineralization	Soil microbial community/functional groups	Process rates‡	Balser <i>et al.</i> (2001)
Supporting	Above-ground net primary productivity	Herbaceous community	Biomass accumulation rate	Reviewed in Schmid <i>et al.</i> (2001)
Supporting	Mineralization and decomposition	Herbaceous community	N leaching or retention; decomposition rate; microbial biomass, etc.	Reviewed in Schmid <i>et al.</i> (2001)

*Studies that calculated total function from each ecosystem service provider as $F_k = \sum f_{ike}$, or a modification thereof.

†Compared observed community level shredding rate against predicted rate based on individual efficiencies of community members to determine that inter-specific interaction enhanced shredding.

‡N₂O, nitrification potential, CO₂, net mineralization, gross NH₄⁺ mineralization.

While I have described it at the scale of populations and communities, the same concepts apply to the level of habitat/ecosystems (Table 1). In fact, this general approach has already been used to measure a wide variety of functions/services (Table 2), although a general framework has just recently been articulated (Balvanera *et al.* 2005). For example, Ostfeld & LoGiudice (2003) measured how efficiently different vertebrate hosts transmit Lyme disease to tick vectors, and then calculated the total human infection rate (or conversely, disease dilution effect) produced by vertebrate communities of differing composition. Guo *et al.* (2000) measured water flow regulation provided by different forest habitats in a Chinese watershed, and used this information to calculate habitat-specific contributions to electric power generation from a hydroelectric power plant. Solan *et al.* (2004) estimated the contribution of different species of benthic marine invertebrates to sediment mixing, and used these data to estimate 'biogenic mixing depth', a determinant of

oxygen concentrations and decomposition rates, for communities of varying composition.

There are other ways of characterizing the functional attributes and importance of ESPs. Another method is to define the 'ecological distance' of ESPs in functional attribute space (Walker *et al.* 1999). This then gives a measure of 'functional attribute diversity' for a community. This measure is useful when it is not practical to measure the efficiency of different ESPs for a given service. An advantage of this approach is that one can subdivide the community into groups of functionally similar (redundant) ESPs and thus predict the resilience of communities to environmental change (Elmqvist *et al.* 2003) or identify guilds exhibiting functional dissimilarity (complementarity). A disadvantage is that the relationship between aggregate function and each ESP is less clear. Characterizing both functional structure and functional attributes of a community would provide the most complete and useful set of information.

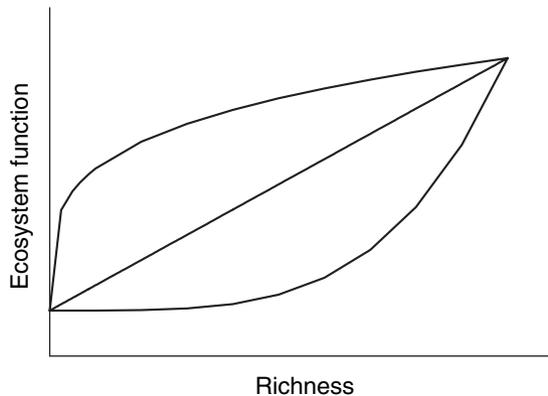


Figure 1 Observed relationships between biodiversity and function can be generated from a simple, but often applicable, model, $F_k = \sum_{j,i,k} f_{j,i,k} = \sum e_{j,i,k} n_{j,i,k}$. In this case, saturation, in which the majority of species add little to total function, would occur when many species are low in abundance, low in efficiency, or both. A linear relationship, in which each additional species adds a unit of function, would occur in even communities with little functional differentiation among species in efficiency, or if species that are low in abundance are high in efficiency and vice versa. An accelerating function would occur when interactions between species enhance their efficiencies (e.g. Duarte 2000). Most experimental studies to date support linear or saturating relationships (Schwartz *et al.* 2000). In natural communities, where extinction order is non-random, the shape of the richness–function relationship also depends on the relationship between response traits that determine sensitivity to environmental factors, and effect traits that determine functional contribution (Larsen *et al.* 2005; Solan *et al.* 2004).

Broaden diversity–function relationship to service-providing communities in real landscapes

Most diversity–function research has focused uniquely on the role of species richness, 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 the spatial and temporal variation of these attributes (Diaz *et al.* 2003; Symstad *et al.* 2003). In addition, the majority of studies have used synthetic, experimental communities that are species-poor, have artificial abundance distributions, and are indirectly rather than directly related to ecosystem services (Schwartz *et al.* 2000; Loreau *et al.* 2001; Ostfeld & LoGiudice 2003). To manage ecosystem services, we need to understand how realistic changes in all of these aspects of community structure, acting singly or together, affect the magnitude and the stability (resilience) of the ecosystem service provided over space and time. More specifically, we need to explore which services and systems exhibit compensatory or stabilizing responses vs. rapid loss of

function, with what frequencies, via which mechanisms, and under what conditions. Below, I detail the specific questions we should be addressing, and then briefly summarize what is known to date.

Compensatory or stabilizing responses

What are the conditions under which aggregate function remains stable due to compensatory responses, despite changes in underlying community structure such as local extinction? What kinds of compensatory mechanisms exist, and how common is each? Are compensatory responses more typical of certain types of communities, ecosystems or functions? Are there thresholds (e.g. of aggregate ecosystem properties like species richness, aggregate abundance) below which compensatory responses no longer operate?

Three known compensatory mechanisms are the portfolio effect, density compensation and functional compensation. The ‘portfolio’ or ‘statistical averaging’ effect is the stabilizing effect of diversity on function that occurs simply through the net effect of random changes in species abundances. Tilman *et al.* (1998) showed theoretically that this effect depends on the relationship between the mean (m) and variance (σ^2) of populations in a community. Given the general relationship, $\sigma^2 = cm^{\zeta}$ (c, ζ are constants), and certain simplifying assumptions (even species abundances with no covariance), diversity confers a stabilizing effect solely from statistical averaging if $\zeta > 1$, a neutral effect if $\zeta = 1$, and a destabilizing effect if $\zeta < 1$. Thus, if $\zeta > 1$, more diverse communities provide more stable services than less diverse communities, just as more diverse stock holdings minimize volatility and thus investment risk (portfolio effect).

Adding covariance between species abundances modifies this general relationship. Density compensation occurs when there are negative correlations between species abundances and enhances stability over that attained purely by statistical averaging. In contrast, positive correlations (e.g. similar responses of a species to a changing environment) negate the effects of statistical averaging and reduce stability (Tilman *et al.* 1998). In experimental plots in a temperate grassland, density compensation presumably played a role in stabilizing aggregate above-ground biomass following a drought, because reduced abundances of certain species led to the competitive release of others (Tilman 1996). A related phenomenon is known as ‘response diversity’ (Elmqvist *et al.* 2003): differential response of species to disturbance stabilizes function. In savanna rangeland communities in Australia, minor species that were functionally similar in trait space (redundant) to the dominant herbaceous species responsible for the majority of ecosystem functions (carbon storage, nitrogen cycling, etc.) were also more resistant to grazing, becoming superior competitors under conditions of high grazing (Walker *et al.* 1999). Too few empirical studies

exist to evaluate whether this interesting interaction between functional traits, response to disturbance and competitive release might be common; what is needed is an accurate characterization of how functional attributes within a community map against sensitivity to disturbance, and how this in turn affects the community composition and aggregate functional response to disturbance. More empirical work is also needed to assess how frequently statistical averaging stabilizes function (i.e. $\bar{z} > 1$) and to disentangle statistical averaging from compensatory responses (Tilman *et al.* 1998). Additional theory is needed to develop predictions for communities with uneven abundance structures.

Finally, functional compensation, or the increase in the efficiencies of individuals as aggregate abundance declines or community composition changes, is another possible stabilizing mechanism. For example, honey bee visitors of apple remove greater amounts of pollen when more pollen is available (Thomson & Goodell 2001). Therefore, individuals are likely to carry larger amounts of pollen on their bodies when bee densities are low, which could lead to larger amounts of pollen transferred per visit (Harder & Thomson 1989), and possibly, to partial functional compensation for the overall lack of pollinators in the orchard.

Many communities in nature may exhibit no compensatory mechanisms that stabilize function. In sea grass communities, removal of the dominant species (*Thalassia hemprichii*) led to loss of additional sea-grass species, rather than compensation, so that overall biomass and diversity declined, reducing the services provided by the seagrass habitat (e.g. carbon storage, erosion and sedimentation control, Duarte 2000). Similarly, no density compensation was observed in either tropical beetle or temperate bee communities as richness diminished in response to habitat loss; reduced numbers of individuals was associated with diminished function for dung burial and crop pollination, respectively (Larsen *et al.* 2005). It is certainly critical to know how often compensatory functional responses do not occur, which types of communities tend not to exhibit such responses, and whether lack of compensatory responses are more common in response to anthropogenic, rather than natural, disturbances. When no compensatory mechanisms exist, rapid loss of function in response to disturbance and changing community composition is more likely.

Rapid loss of function

When function is rapidly eroded in response to changing community composition (e.g. Fig. 1, linear and accelerating curves), how often is it due to preferential loss of species that are most functionally important? How often is it due to the loss of species that facilitate or complement the functional properties of other species? How often is

function lost through massive changes in abundance structure, rather than species loss? Under what circumstances could compensatory mechanisms mitigate rapid loss of function? Here I use the term 'species loss' to refer to local, not global, extinctions because populations, not species, are the fundamental functional unit (Balmford *et al.* 2003; Luck *et al.* 2003).

The order of species loss is often non-random, particularly in response to anthropogenic impacts. Increasingly, models and empirical studies suggest that the identity and the order of species loss or gain are critical to effects on function. Ostfeld & LoGiudice (2003) simulated the effects of changing vertebrate species composition on Lyme disease dilution for humans. They found an approximately linear decrease in Lyme disease dilution when the extinction sequence of vertebrate host species mirrored that occurring in nature with decreasing fragment area; in contrast, when extinction sequences were randomly generated, loss of function was initially small but ultimately large (saturating richness–function curve, Fig. 1). Rapid loss of function (accelerating richness–function curve, Fig. 1) will occur if the most important species are lost first. We found that the most important crop pollinators were most likely to be lost along a gradient of agricultural intensification in California, while the dung beetle species responsible for burying the most dung were also lost first on recently created islands of decreasing area in Venezuela (Larsen *et al.* 2005). In both cases, response and effect traits were correlated, and an accelerating curve provided the best fit to the richness–function data. When response and effect traits are correlated, compensatory mechanisms are unlikely to mitigate the loss of key species (Solan *et al.* 2004). Using simulations, these authors found that imposing density compensation did not alter richness–function curves if extinction order was determined by response traits, while it completely compensated for species loss when extinction sequences were random.

Ordered extinction sequences could also have large effects on function if species loss is associated with loss of inter-specific interactions that enhance function through complementarity or facilitation. For example, loss of complementarity may be the reason for greater invasibility of low vs. high diversity temperate grasslands in California; here low-diversity subsets entirely lack whole functional groups found in higher diversity assemblages (Zavaleta & Hulvey 2004). Similarly, in six plant and animal assemblages, complementarity in functional attributes led to rapid loss of functional diversity even under random extinction order; this pattern was significantly enhanced by imposing trait-dependent extinction sequences (Petchey & Gaston 2002). Finally, Jonsson *et al.* (2002) observed a greater loss of function than expected in experimental communities of leaf-shredding invertebrates assembled to mimic observed extinction order in response to increasing acidification and

pollution. They attributed this rapid loss of function to loss of inter-specific interactions facilitating leaf shredding.

Function can also be lost through massive changes in abundance structure rather than outright extinction. In the oceans, numerous examples of 'ecological extinction' exist in which species are so diminished through overharvesting that they no longer exert key functional roles structuring these ecosystems. Striking examples include the reduction in filter-feeding oyster populations to 1–2% of their former size in the Chesapeake Bay, leading to eutrophication of the Bay (Newell 1988; Jackson *et al.* 2001), and; the extensive reduction and subsequent recovery of kelp forest ecosystems in the Pacific Northwest oceans in response to the reduction and recovery of sea otter populations from hunting (Estes & Palmisano 1974; Jackson *et al.* 2001).

It is clear from the limited data available that the answers to these questions will be both system and service-dependent, and studies of a broad array of systems and services are needed. Diaz *et al.* (2003) review a variety of applicable techniques, including monitoring patterns in nature, removal experiments and creation of synthetic assemblages. An approach that combines observations of natural disassembly of communities in response to disturbance with targeted experiments (e.g. Zavaleta & Hulvey 2004) and simulations (e.g. Ostfeld & LoGiudice 2003; Larsen *et al.* 2005) will be most informative and realistic for understanding ecosystem services. Such an approach is also most likely to identify the key environmental factors affecting service provision over space and time, which is essential information for devising management plans.

Key environmental factors affecting service provision over space and time

There are two complementary approaches for studying the environmental factors that affect the magnitude and variability of ecosystem services across the landscape. The first is to focus on the abundance of an important ESP (ESP-centred approach), and the second is to focus on the

function as a whole, irrespective of fluctuations in individual ESPs (function-centred approach). The choice of an ESP- vs. function-centred approach should depend on the results of the functional inventory. If individual ESPs are highly uneven in their functional contributions (e.g. dominated by a single species, Solan *et al.* 2004), an ESP-centred approach would be useful. In contrast, if functional structure is even ($f_{jk} \approx f_{pk}$ for all j, p), or interactions among ESPs are thought to greatly alter function, or the community is made up of ESPs that differ widely in functional traits (complementary groups), then a function-centred approach is indicated, although both should perhaps be used (Table 3).

In the ESP-centred approach, we would use traditional tools in ecology/conservation biology to identify the environmental variables affecting the distribution, abundance and persistence of selected ESPs, in order to develop spatially explicit management plans for these populations, analogous to the set of ecological knowledge required to develop species recovery plans (e.g. Bay Checkerspot butterfly, http://ecos.fws.gov/docs/recovery_plans/1998/980930c.pdf, Ehrlich & Hanski 2004). In the function-centred approach, use of multivariate techniques can be a powerful approach for identifying the environmental factors that influence aggregate function and its variability. For example, Kremen *et al.* (2004) found that both the magnitude and stability of crop pollination services provided by native bees depended on the proportion of upland natural habitat within several kilometres of the farm site, and not on other local and landscape scale variables. This finding can be used to set conservation targets (*sensu* Margules & Pressey 2000) to sustain the service in the landscape.

Spatial and temporal scale of ecosystem services

Most ecosystem services can be broadly classified as operating on local, regional, global or multiple scales (Table 1). For example, native parasitoids and predators that provide pest control on crops generally operate at a local scale, while forests contribute to climate regulation at

Table 3 Selection of the ESP-centred or function-centred approach should depend on how evenly functional contribution is distributed among community members, how functionally dissimilar ESPs are, and whether interactions among community members strongly influence function. If only a few community members contribute the majority of function (low evenness) and there is little differentiation in functional traits (low complementarity), then focusing on key ESPs is advantageous. If there are interactions that enhance (e.g. facilitation) or depress (e.g. competition) function, then a function-centred approach should be used. These two approaches are not mutually exclusive and could be used together to advantage

	Weak/no interactions				Strong interactions			
	Even		Uneven		Even		Uneven	
Functional structure	Even		Uneven		Even		Uneven	
Functional traits	Similar	Dissimilar	Similar	Dissimilar	Similar	Dissimilar	Similar	Dissimilar
ESP-centred	N	N	Y	Y	N	N	Y	Y
Function-centred	Y	Y	N	Y	Y	Y	Y	Y

local, regional and global scales (local: shading; regional: rainfall patterns and albedo; global: carbon sequestration). Understanding the spatial scales at which ecosystem services operate will be essential to developing landscape-level conservation and land management plans. How much of a watershed area must be maintained in 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? Conversely, up to what distances might adjacent land uses affect the capacity of forest and soil ecosystems to purify water (Houlahan & Findlay, 2004) or of natural habitat to provide pest control and pollination services? The answers to these questions will determine how set-asides should be distributed, and areas zoned for different land uses, in order to protect and manage the service.

Different providers of the same ecosystem service may operate across a range of spatial and temporal scales. For example, there are 35 bird predators on spruce budworm, a major pest in temperate forests, and they span a wide range of body sizes and foraging abilities (Holling 1988). Larger predators may switch to preying on spruce budworm only when it occurs in large aggregations, thus providing regulation under outbreak conditions, while smaller predators control the pest at lower densities (Peterson *et al.* 1998). Different species of pollinators can begin flight at different times of the day as determined by their body size, warm-up rates and allowed ambient flight temperature (Stone & Willmer 1989); this also affects daily and seasonal activity periods and the delivery of pollination services under different weather and microclimate conditions (Klein *et al.* 2003). Peterson *et al.* (1998) propose that species performing the same function but operating at different spatio-temporal scales will provide resilience to ecosystem services. An alternate view is that resilience will be achieved across space and time when assemblages of competing species are largely composed of species with intermediate dispersal abilities. Such assemblages will be higher in diversity, and thus redundancy and resilience, than assemblages of low or high dispersal, in which competitive exclusion could reduce diversity (Loreau *et al.* 2003).

For population-based services like pest control and pollination, determining the area over which services are provided requires understanding the dispersal and foraging movements made by the ESPs. As this type of biological data is often difficult to obtain, particularly for multiple species within a guild, other methods may be necessary, including determining the scale of the best model (Pearman 2002), matching the scale at which the organism perceives its environment to the scale of the landscape (Brooks 2003) or conducting macro-ecological analyses that derive predictive relationships between traits like body size or home

range size and foraging movements (Holling 1992). Studies of services should ideally be conducted at multiple, nested scales, as environmental effects on them may be uncorrelated across scales (Sayer & Campbell 2004).

USING ECOLOGICAL DATA IN VALUATIONS AND ENVIRONMENTAL DECISION-MAKING

Calculations of economic values of ecosystem services at the global scale indicate the economic importance of services and have put the concept 'on the map' (Daily *et al.* 2000; Millennium Ecosystem Assessment 2003; Palmer *et al.* 2004). As they often have large uncertainties (Naylor & Ehrlich 1997), however, they are of little utility in land-use planning (Reid 2001). The use of local ecological data leads to valuations that can influence land-use decisions on a scale at which they are typically made. 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 found that the value of forest habitat for water regulation had a higher monetary value than its timber value, and developed a price for compensating landowners for foregone timber based on the marginal value of electrical power produced when a unit of a given habitat type was conserved.

For decision-making, we need to know the additional (marginal) value of ecosystem services produced by conserving another unit of habitat (Dasgupta *et al.* 2000), as in the Chinese water regulation example. Many ecological phenomena demonstrate nonlinear threshold effects (Levin 1999); this has implications for the economics of land-use planning. For example, suppose that a service such as water purification increases sigmoidally with increased habitat conservation (Fig. 2a). In this case, the marginal benefits of protecting additional habitat units will be highest in the steep region of the service-habitat curve (Fig. 2b), and marginal benefits from the service will tend to exceed marginal costs of habitat acquisition in the region near the threshold. The target for land acquisition should therefore fall between the upper and lower boundaries of the threshold (Fig. 2b, arrows), suggesting that understanding the relationship between ecosystem service and habitat area will assist in making sound economic decisions. Because trade-offs occur between different ecosystem services and land uses, it will also be necessary to bring ecological knowledge about multiple ecosystem services to decision-making (DeFries *et al.* 2004).

Armsworth & Roughgarden (2003) recommend basing land-use decisions not simply on the marginal value of ecosystem services added by an additional unit of habitat,

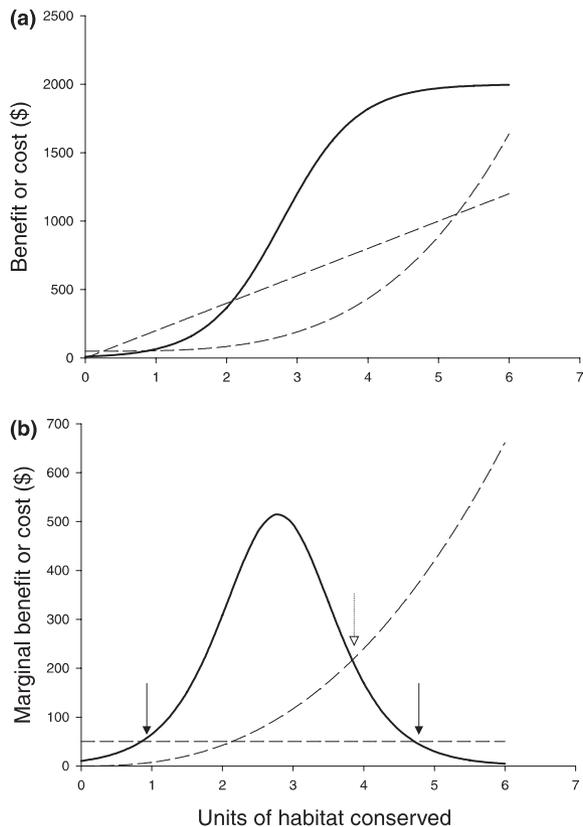


Figure 2 (a) A hypothetical relationship between the value of water filtration services provided and the area of land conserved (solid line), showing a threshold effect. The two dashed lines represent the cost of acquiring land under two scenarios, constant costs or accelerating costs. (b) The derivative of the ecosystem function–land area relationship shown in (a) is the marginal service value (solid line) of each unit of habitat; marginal value peaks at the inflection point in (a). Wherever the marginal value exceeds the marginal cost of conserving an additional land unit (dashed lines representing different cost functions above), it is beneficial to preserve habitat (between solid arrows for constant marginal cost; up to open arrow for accelerating marginal cost).

but also on the additional stability to ecosystem services that another unit of habitat would add. Therefore, it is important to understand not only the relationship between ecosystem service and habitat area, but also the relationship between the *variability in ecosystem service* and the habitat area, another relationship that may demonstrate nonlinearity.

Finally, ecological information is needed in order to design both policies and markets properly. For example, under the Endangered Species Act (ESA), developers in certain states can ‘mitigate’ their take of endangered species by paying for conservation credits in a conserved natural area (conservation bank) that contains a population of the species (Bean *et al.* 1999). Conservation banks, however,

might not actually contribute to the recovery of an endangered species if the population ‘taken’ by development is not ecologically equivalent to the one in the conservation bank (e.g. the destroyed population is a source, while the banked one is a sink, *sensu* Pulliam 1988). Ecological information is therefore needed to determine the value of each species unit in the conservation bank, and set allowed trades and market prices accordingly. Similarly, 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. The decision to include carbon offsets from land management practices in the Kyoto Protocol already required extensive scientific support; however, a much greater understanding of the fundamental biogeochemical processes involved in greenhouse gas regulation will be needed to develop a detailed accounting system to implement the policy and monitor compliance (Watson *et al.* 2000).

CONCLUSION: APPLYING THIS FRAMEWORK IN THE REAL WORLD

I conclude with an example of work-in-progress: we are applying this four-step framework to develop plans to manage pollination services supplied by wild bees in California, the most important agricultural region in terms of value of food produced in North America. Pollination by bees is required for 15–30% of US food production. In large-scale agriculture, most farmers import colonies of managed honey bees, *Apis mellifera*, to supply pollination needs, but wild, non-*Apis* bees may also contribute to crop pollination. (1) We conducted a functional inventory to characterize the functional contributions of wild and managed bees servicing watermelon, tomato and sunflower crops (Kremen *et al.* 2002a,b; Greenleaf 2005). We found that wild bee communities alone (without the addition of managed honey bees) can provide partial or complete pollination services or enhance the services provided by honey bees through behavioural interactions. (2) These services are rapidly eroded (e.g. accelerating curve of Fig. 1) in response to agricultural intensification. The most important pollinating species are lost first, and other species do not compensate by increasing in abundance (Larsen *et al.* 2005). (3) The proportion of wild habitat (chaparral and oak-woodland) within 1–2 km of a farm strongly explains the magnitude and the stability of the service provided, as well as the diversity, abundance and productivity of foraging and nesting bees (Kim 2004; Kremen *et al.* 2004; Greenleaf 2005). (4) This scale closely matches the predicted maximal foraging distance of the largest bees in the community (Kremen *et al.* 2004).

These findings have important economic implications. Honey bee stocks have steadily declined for the past 50 years due to diseases (USDA-NASS 1997). Farmers already derive value from wild bee pollination services, and more importantly, wild bees provide an insurance policy for farmers and consumers in the event of further decline, or even total loss, of managed honey bee stocks (Southwick & Southwick 1992; Kremen *et al.* 2002b). We are using the relationship between pollination services and natural habitat to establish targets for conservation and restoration (Kremen *et al.* 2004). We are developing restoration and farm management protocols based on spatial and temporal availability of key floral resources in natural and farmed areas of the landscape (Kremen *et al.* 2002a; Vaughan *et al.* 2004). We are creating spatially explicit models based on resource availability, resource needs, and foraging scales, to develop alternative scenarios for managing the agro-natural landscape for pollination function (Regetz and Kremen, in prep.). Finally, we are providing this ecological information to landowners and land-managers through workshops, manuals (Vaughan *et al.* 2004) and demonstration sites.

As human populations increase over the coming decades, managing ecosystems for services will become increasingly important to prevent both shortages of water, energy and food, and increases of disease and global conflict (Millennium Ecosystem Assessment 2003). The potential demand for managing landscapes for services is enormous. For example, 13% of the terrestrial land surface could be managed for urban water use alone (Reid 2001). Over 3 million ha of land could be reforested for carbon sequestration per year, once the Kyoto Protocol enters into force as expected in 2005 (Niles *et al.* 2002).

Developing management plans for services that includes a detailed understanding of their ecology is feasible, but it requires a considerable investment in research, akin to that devoted to agriculture, medicine and defence. How could this be achieved in practice? A strategic plan would be to select a spatial hierarchy of replicated study sites (sites within landscapes, landscapes within ecosystems and ecosystems within biogeographical realms) and to study a representative set of services with standardized methods at each site. While the initial costs of establishing such a global network would be high, maximum value per effort could be obtained by such a design, and some large-scale networks to study ecosystem services and functions already exist (e.g. Hector *et al.* 1999; Millennium Ecosystem Assessment 2003; Settele *et al.* 2005). This design would provide gains in on-the-ground efficiency and statistical power, permit detection of general patterns within or between scales, and allow assessments of trade-offs between services (Arnqvist & Wooster 1995; Sayer & Campbell 2004). Conducting this ecological research not in isolation, but as an integrated component of teams comprising a diversity of both

scientific disciplines and resource users, would provide a mechanism for broad dissemination of knowledge, and set the stage for adaptive management (e.g. Biggs *et al.* 2004; see also Sayer & Campbell 2004; Robertson *et al.* 2005). Ecologists should mount a massive awareness campaign to convince society of the importance of ecosystem services and to demand the resources for their study – nothing less than our human future is at stake.

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