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REVIEW AND SYNTHESIS

Understanding relationships among multiple ecosystem services

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Abstract

Ecosystem management that attempts to maximize the production of one ecosystem service often results in substantial declines in the provision of other ecosystem services. For this reason, recent studies have called for increased attention to development of a theoretical understanding behind the relationships among ecosystem services. Here, we review the literature on ecosystem services and propose a typology of relationships between ecosystem services based on the role of drivers and the interactions between services. We use this typology to develop three propositions to help drive ecological science towards a better understanding of the relationships among multiple ecosystem services. Research which aims to understand the relationships among multiple ecosystem services and the mechanisms behind these relationships will improve our ability to sustainably manage landscapes to provide multiple ecosystem services.

Keywords

Ecosystem services, ecosystem management, resilience, social-ecological systems.

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INTRODUCTION

Humanity has expended substantial effort to engineer ecosystems to cheaply and reliably produce desired ecosystem services such as food, timber, and fibre (Foley *et al.* 2005; Kareiva *et al.* 2007; Monfreda *et al.* 2008; Ramankutty *et al.* 2008). (See Side bar for definition of ecosystem services and other key terms.) However, these efforts have often overlooked the fact that landscapes simultaneously produce multiple ecosystem services that interrelate in complex dynamic ways (Peterson *et al.* 2003; Chan *et al.* 2006; Rodriguez *et al.* 2006; Brauman *et al.* 2007). Thus, an unintended consequence of human domestication of ecosystems has been unexpected or undesirable declines in other ecosystem services. Globally, this has led to an increase in a few services, such as food and timber, and a decline in most other services such as flood control, genetic resources, or pollination (Millennium Ecosystem Assessment 2005). Sometimes, an overly-narrow focus on a limited set of ecosystem services has even led to regime shifts with unexpectedly sudden losses of other ecosystem services (Gordon *et al.* 2008). These declines and sudden shifts are problematic because demand for reliable provision of almost all ecosystem services is increasing (Millennium Ecosystem Assessment 2005).

Consequently, recent studies have called for increased attention to development of a theoretical understanding behind the multiple and non-linear relationships among ecosystem services (Turner *et al.* 2003; Kremen & Ostfeld 2005; Tallis & Kareiva 2005; Carpenter *et al.* 2006b, 2009). While managing multiple ecosystem services simultaneously is important, it is also extremely challenging. Although scientists have assessed threats to ecosystem services (Tilman *et al.* 2001; Millennium Ecosystem Assessment 2005), calculated the value of services provided (Gallai *et al.* 2009), (Costanza *et al.* 1997), mapped supply and demand (van Jaarsveld *et al.* 2005; Deutsch *et al.* 2007), and assessed the current and potential future status of ecosystem services (Carpenter *et al.* 2006a), we still have relatively little understanding of the ecology behind the provision of ecosystem services (Kremen & Ostfeld 2005).

To meet the growing demand for science about managing multiple ecosystem services, an increasing number of studies have examined how multiple ecosystem services change with land use and land cover across a landscape. Barbier *et al.* (2008) showed how conversion of mangroves to shrimp farming changes the supply of a set of ecosystem services. As an increasing proportion of a region's coastal mangroves are converted the net benefits of these services begin to decline due to the loss of ecosystem services such as coastal protection, wood product collection, and habitat support for offshore fisheries (Barbier *et al.* 2008). In this case, examining multiple ecosystem services provided by mangroves and those provided by shrimp farming showed that socially suboptimal choices would result if only the value of the shrimp production is taken into account. Similarly, Pretty *et al.* (2006) analyzed 280 case studies of how small scale investments in agriculture in developing countries also improved water balance, carbon sequestration and water quality, showing that some types of agriculture can improve multiple ecosystem services simultaneously. Naidoo & Ricketts (2006) mapped the spatial costs and benefits of conservation in a region where different types of forest could be converted into agricultural land. They assessed the value of ecosystem services in forested areas, including bushmeat, pharmaceuticals, carbon storage, existence value, and the expected value of conversion to agriculture and found a high degree of spatial variability in the costs and benefits, as well as in the optimal decision about land use conversion indicated by the net value of services provided.

Several recent papers explore the spatial patterns of provision of multiple services across landscapes, focusing on spatial concordance among services as evidence of win-win opportunities for conservation of multiple ecosystem services and biodiversity, a traditional conservation target (e.g. Chan *et al.* 2006; Egoh *et al.* 2008; Naidoo *et al.* 2008; Nelson *et al.* 2009). The results of these studies intimate that there are important relationships among ecosystem services, even if the authors have not explicitly been looking for such. That is, some services often appear together on the landscape while others appear only opposite one another. Despite a number of these studies, there remains disagreement about whether spatial concordance of ecosystem services is rare (Naidoo *et al.* 2008; Tallis *et al.* 2008) or not (Nelson *et al.* 2009), and general rules about concordance have yet to be determined. Chan *et al.* (2006) found only weak associations (both positive and negative) between the priority areas for biodiversity conservation and provision of the six ecosystem services in the Central Coast ecoregion of California, United States. Egoh *et al.* (2008) mapped provision of five ecosystem services (surface water supply, water flow regulation, soil accumulation, soil retention, and carbon storage) across South Africa to assess the relationship between the services and determine whether primary production might be a good surrogate measurement for the distribution of ecosystem services. The authors found that most services were not good surrogates for one another, indicating that one cannot manage for one service and expect that this management will necessarily benefit other services as well (Egoh *et al.* 2008). However, it may be that some types of management can actually change the relationships among ecosystem services, creating opportunities to enhance multiple services simultaneously. These studies have enhanced our knowledge about which services we might examine for relationships because they identify services that commonly appear together on the landscape and the conditions in which this happens; however, they have typically not assessed the mechanisms behind the relationships between services.

Although there is evidence of relationships among ESs, and that these need to be better understood to improve ecosystem management, the science that takes these relationships into account remains limited (Tallis *et al.* 2008). Most science implicitly uses as a simplifying assumption the notion that ecosystem services do not have significant and variable relationships with one another. Even the Millennium Ecosystem Assessment assessed most services individually and only in a few instances dealt with interactions among more than two services (Millennium Ecosystem Assessment 2005). Second, when relationships between ecosystem services are studied, scientists have typically addressed only two services at a time. Finally, because ecosystem services can be difficult to measure directly, scientists have tended to use land use/land cover as a proxy for the provision of services (Nelson *et al.* 2009) even though the relationships between land use/land cover and service provision are largely untested for most services in most regions of the world (Naidoo *et al.* 2008). These studies typically assume a linear relationship between ecosystem structure and provision of services, an assumption that is unlikely to be widely valid (Koch *et al.* 2009) and one that precludes investigating any relationships among the services themselves that is not the direct result of competition for, or sharing of, land. The result is that our understanding of the relationship between ecosystem processes and provision of services remains fairly dim for most ecosystems and most services (Carpenter *et al.* 2009). Thus, we don't know much about when to expect trade-offs or synergies, the mechanisms that cause them, or how to minimize trade-offs and enhance synergies.

Without knowledge about the relationships among ecosystem services, we are at risk of incurring unwanted trade-offs, squandering opportunities to take advantage of synergies, and possibly experiencing dramatic and unexpected changes in provision of ecosystem services. In this paper, we suggest a typology of relationships among ecosystem services and develop three propositions for urgently needed research based on this typology.

A TYPOLOGY OF ECOSYSTEM SERVICE RELATIONSHIPS

We propose that ecosystem service relationships be classified based on the two types of mechanisms causing them: (1) effects of drivers on multiple ecosystem services (i.e. common drivers) and (2) interactions among ecosystem services (Figs 1 and 2). Management interventions such as land use change, fertilization, or the building of trails, can drive change in one or more ecosystem services. These drivers of ecosystem service provision can affect a single ecosystem service, with only trivial effects on other services of interest, or they can have significant effects on multiple services at once (shown along the *x*-axis of Fig. 2). For example, building infrastructure to encourage agricultural tourism by allowing people to watch the production of maple syrup and purchase maple syrup products enhances the supply of cultural ecosystem services such as recreation without effecting maple syrup production (Sector 1 in Fig. 2). On the other hand, increasing fertilizer use to improve crop production can have a significant negative effect on local provision of clean water in addition to the intended effect of increasing crop yields (Sector 2). These effects of drivers on provision of multiple ecosystem services can be in opposite directions (i.e. diminishing one service while enhancing the other), leading to a trade-off wherein provision of one service increases while another declines, such as in the case of fertilizer use to improve crop yields. The effects of a driver can also be in the same direction for two services (enhancing both services or diminishing both services). For example, response to a driver that aims to enhance one service can lead to a synergy, wherein multiple ecosystem services respond positively to change in the driver, such as when wetland restoration improves both water quality and flood control (Hey 2002; Zedler 2003).

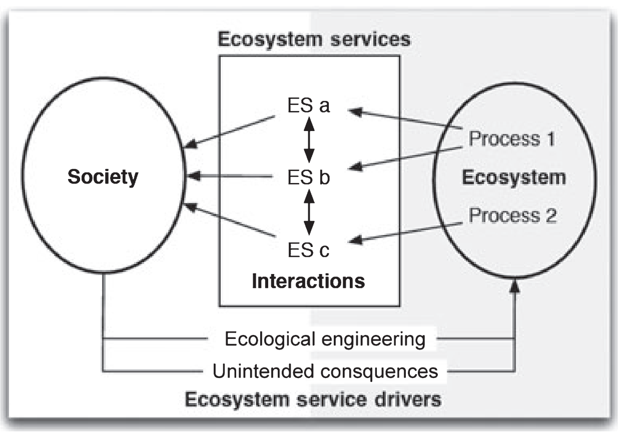

Figure 1 Ecosystem services are benefits that people receive from ecosystems. They can usefully be conceived as part of a social-ecological system, for in the absence of people there are no services, and people often modify ecosystems to enhance the production of specific services.

Along with effects of drivers on multiple ecosystem services, relationships among services can be caused by direct interactions among the services (shown along *y*-axis of Fig. 2). In the cases mentioned above, this interaction (between cultural services and maple syrup production, water quality and crop yield, or water quality and flood control) is weak or non-existent. In other cases, the interaction among services can be unidirectional (the level of provision of service A affects the level of provision of service B) or bidirectional (the level of provision of service A affects the level of provision of service B, and the level of provision of service B affects provision of service A). As with the effects of drivers on services, bidirectional interactions can drive service provision in the same direction (increasing provision of service A enhancing provision of service B or decreasing provision of service A diminishes provision of service B) or opposite directions (enhancing provision of service A diminishes provision of service B or decreasing provision of service A enhances provision of service B). For example, a positive unidirectional interaction is the one by which retaining forest patches near coffee increases pollination, which in turn increases coffee production (Ricketts *et al.* 2008); increased coffee production does not have an impact on pollination. A unidirectional negative interaction exists when, for example, afforestation enhances carbon sequestration, but the process of tree growth increases evapotranspiration, decreasing water availability (Fahey & Jackson 1997; Engel *et al.* 2005). A bidirectional interaction (Sector 5) among ecosystem services can be found in small-scale dryland agriculture. Many of these systems, especially in sub-Saharan Africa, are characterized by land degradation where over-extraction of biomass reduces soil organic matter and increases erosion, leading to lower yields, which in its turn leads to even increased pressure on the land. Management practices that aims to break this spiral (for example, conservation tillage, terracing, increased use of manure) can enhance erosion control which improves crop yields and which lead to further increased incentives to invest in the land thus further improving erosion and yields (Gordon & Enfors 2008).

There are many other examples of the types of relationships in this typology in the literature (Table 2). A unidirectional, positive interaction among services who also share a driver (Sector 4) is found in marine protected areas near coral reefs. In marine protected areas that have been set aside to protect fish populations for tourism, conservation of fish populations also maintains the regulating ecosystem function of algae grazing. Algae-grazing

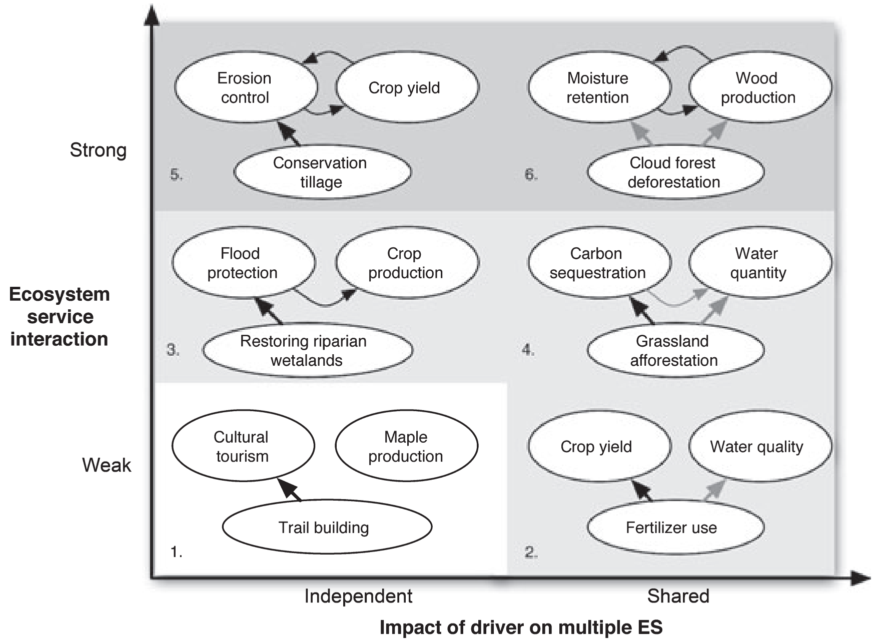

Figure 2 The supply of ecosystems services can be related either due to interactions between ecosystem services, or due to responding to the same driver of change. Black arrows indicate a positive effect and grey a negative effect.In the lower left-hand sector (Sector 1), a driver (trail-building) affects cultural tourism (Service A), which has no interaction with maple syrup production (Service B). In the Sector 2, the driver affects both services, but these services have no interaction with one another. In the example presented here, fertilizer use has a positive effect on crop yield and a negative effect on water quality. However, the driver also might affect both positively or both negatively. Moving up along the *y*-axis, Sectors 3 and 4 show examples in which the services have a unidirectional interaction. That is, the level of provision of service A affects the level of provision of service B, but not vice versa. Sectors 5 and 6 show a bidirectional interaction among services in which the level of provision of service A affects the provision of service B and the level of provision of service B affects the provision of service A. In all cases, this interaction can be positive or negative.

fish help maintain coral reef and help them recover from disturbance such as bleaching events or storms (Hughes *et al.* 2005). Intact coral reef in turn provide more habitat for fish populations, enhancing the grazing functioning, as well as improving reef quality for tourism (Bellwood *et al.* 2004). Several recent studies have examined the synergy between preserving forested or other natural land in agro-ecological landscapes and agricultural production, suggesting a mechanism involving a bidirectional interaction among ecosystem services without a shared driver (Sector 3). For example, preserving uncultivated land increases agricultural yields per hectare by increasing pollinator habitat (and thus pollination) in Canadian canola fields (Morandin & Winston 2006). At the same time, preserving uncultivated land reduces the amount of land in production and might decrease agricultural production across the landscape. Similarly, Olschewski *et al.* (2006) found that preserving forest patches near coffee plantations could increase coffee production. Priess *et al.* (2007) suggest as a possible mechanism that forests close to plantations increases pollinator populations and thus increase potential pollination and fruit set of coffee.

Implications of the typology for ecosystem management

Knowing where in this typology an ecosystem service relationship fits helps distinguish among the mechanisms behind apparent relationships between ecosystem services, which can improve our ability to manage trade-offs and synergies between services. For example, if we know that a trade-off among two services is caused by a shared driver and that there is no true interaction among the services involved, then management must address the driver and its effects on one or both services. If, on the other hand, the trade-off is initiated by the effect of a shared driver, but enhanced by a true interaction among the services, then simply managing the driver is unlikely to truly minimize the trade-off in the long-term. Unfortunately, most ecosystem service science does not examine mechanisms behind ecosystem service relationships in depth and cannot distinguish among the causes of typical relationships. In Fig. 2, the effect of drivers and interactions in Sectors 2, 3, and 4 might all lead to a relationship among services that appears similar (e.g. a trade-off), but would require very different management strategies to effectively address the relationship. If scientists only quantify trade-offs and synergies at one point in time or only examine spatial concordance among multiple services, we risk making incorrect assumptions about the mechanisms behind these relationships and therefore managing them ineffectively.

THREE PROPOSITIONS FOR MANAGING RELATIONSHIPS AMONG ECOSYSTEM SERVICES

The literature we have reviewed here illustrates that ecosystem services can interact directly or appear to interact through the impact of a shared driver, but we have limited theory or general rules about these relationships and their implications for management of ecosystem services. The typology we developed is a step in that direction. Here, we further suggest three propositions to drive empirical data collection and analysis in future ecosystem service research. These propositions are presented as hypotheses; testing them will deepen our understanding of how ecosystems function and improve ecosystem management.

The first proposition deals with the importance of quantifying the provision and use of multiple ecosystem services across landscapes and through time to build a deeper understanding of how services are bundled together and the identification of key interactions. Without this knowledge, we are likely to overlook opportunities to take advantage of synergies among services and will increase our risk of incurring unnecessary ecological trade-offs. The second proposition deals explicitly with synergies and trade-offs among multiple ecosystem services, and how small changes in the relationships among services can create big opportunities for management. The third proposition addresses the role of regulating ecosystem services for stability and resilience of the flow of other ecosystem services.

Proposition 1: Relationships among multiple ecosystems services are better identified and assessed by integrated social-ecological approaches than with either social or ecological data alone.

Ecosystem services are produced by ecosystems and used by people. Consequently, approaches to ecosystem service assessment that focus on either social or ecological factors in isolation will not accurately assess the provision and use of ecosystem services.

Land use/land cover is often used as a proxy to quantify provision of ecosystem services. However, existing systems of land cover classifications substantially simplify human influence on the landscape (Ellis & Ramankutty 2008). Many management actions, including the re-introduction of wolves to Yellowstone National Park, the amount of fertilizer used on agricultural fields, and the use of conservation tillage, affect the relationships among ecosystem services but are invisible to most simple land cover categories, indicating that simple land use/land cover proxies might not adequately capture crucial information needed to predict provision of ecosystem services. Similarly, land cover classifications often overlook small green spaces, such as urban gardens, which generate key urban ecosystem services (Colding *et al.* 2006). Including social data, such as census statistics or information about management and use of ecosystem services in addition to their provision, would allow insights into the role of social factors known to drive ecological functioning, such as population density, wealth, and inequality, to complement the ecological factors (Mikkelson *et al.* 2007).

Research in this area should ask whether there exist consistent sets of ecosystem services associated with particular social-ecological systems in addition to those associated with particular land use/land cover categories. It may also be useful to investigate whether a re-classification of land cover into more social-ecological categories such as anthromes (Ellis & Ramankutty 2008) would improve identification of clusters of ecosystem services that often appear together. Further, by examining how ecosystem service provision changes within a land use/land cover category, scientists might be able to tease out information about the relative influence of social and ecological drivers. (See Table 2 for other relevant research questions.)

Proposition 2: Understanding the mechanisms behind simultaneous response of multiple services to a driver and those behind interactions among ecosystem services can help identify ecological leverage points where small management investments can yields substantial benefits.

The linkages among ecosystem services that create synergies and trade-offs are not fixed, but can shift through time due to change in ecosystem processes or policies that address ecosystem services. For example, creation of riparian buffers alters the trade-off between agricultural production and water quality by limiting the effect of the driver (fertilizer use) on water quality, but does not affect the impact of the driver on agricultural yields. Thus, in some cases, we are not limited to simply responding to existing synergies and trade-offs, but can actually manage their strength and even their existence. Understanding the ecological processes that structure the connections between ecosystem services can help us learn more about when we can attempt to mitigate trade-offs and enhance synergies.

Determining the cause of a relationship among services based on a study which tracks only spatial concordance among ecosystem services can be difficult. That is, without studying the mechanisms behind ecosystem service relationships, one cannot tell whether the relationship is due to the effect of a shared driver acting on two or more services or whether it is due to a true interaction among services or a combination of these effects. Without understanding the cause of the relationship, it is difficult, if not impossible, to properly manage the strength of trade-offs and synergies, let alone their existence.

Our analysis of drivers and interactions among multiple services illustrates a number of cases where it is possible to create synergies or avoid trade-offs by manipulating ecosystem service drivers (Table 1). Agricultural landscapes, in particular, provide many examples of management that can either enhance or degrade multiple ecosystem services, such as nutrient management, which can affect both crop yields and nutrient runoff to aquatic ecosystems. With an anticipated need to double food production in the coming decades (Tilman 1999) and simultaneous demand for increased provision of other services from agroecosystems (Millennium Ecosystem Assessment 2005), better management of ecosystem services in agricultural landscapes is important (Gordon *et al*. In press). However, general rules about when to expect synergies among ecosystem services, how to create them, and how to take advantage of them, even in relatively well-studied agricultural landscapes, are lacking.

For ecosystem services of interest, identifying where they are situated in the typology with respect to multiple other services will improve our understanding of where to invest in order to capitalize on synergies or reduce trade-offs. For example, investing in small scale technologies that improve soil moisture availability in dryland sub-Saharan agriculture seems to be a crucial entry point for reverting land degradation, reducing erosion and increasing carbon sequestration while simultaneously increasing crop yields (Enfors & Gordon 2007; Enfors *et al*. 2008). Including cover crops and deeply-rooted crops can further enhance these benefits. At the landscape scale, forest patches in agricultural landscapes can improve pollination and pest control with positive effects on crop yields (Bodin *et al*. 2006; Kremen *et al*. 2007) and vegetated patches along river banks can attenuate trade-offs between crop yield and water quality (Sharpley *et al*. 1994). Analyzing the contextual details of these relationships to determine the conditions under which they hold true is complex and requires the synthesis of multiple case studies.

Research needed in this area includes long-term monitoring of the provision and flow of ecosystem services across landscapes, focused on the mechanisms behind relationships among services. This type of monitoring can help empirically identify common patterns of tradeoffs and synergies among sets of ecosystem services and will help us understand whether and how these relationships change with time, management, and scale.

Proposition 3: Managing relationships among ecosystem services can strengthen ecosystem resilience, enhance the provision of multiple services, and help avoid catastrophic shifts in ecosystem service provision.

Interactions between ecosystem services create the potential for regulating or destabilising systems of ecosys-

Table 1 Examples of ecosystem service relationships

Sector	Driver	Service A	Service B	Shared driver	Response type	Interaction type	Synergy or trade-off	Reference
1	Trail building	Cultural tourism	Agricultural production	No	–	None	None	(Brscic 2006)
2	Fertilizer use	Crop production	Water quality	Yes	Opposite	None	Trade-off	(Carpenter *et al*. 1998)
2	Wolf re-introduction	Nature tourism	Floodplain maintenance	Yes	Similar	None	Synergy	(Wolf *et al*. 2007)
3	Restoring riparian vegetation	Flood control	Crop production	No	–	Unidirectional, positive	Synergy	(Kramer *et al*. 1997)
3	Maintaining forest patches close to coffee plantations	Pollination	Crop production	No	–	Unidirectional, positive	Synergy	(Ricketts *et al*. 2008)
4	Wetland restoration	Flood control	Water quality	Yes	Similar	Unidirectional, positive	Synergy	(Zedler 2003)
4	Afforestation	Carbon sequestration	Water quantity	Yes	Opposite	Unidirectional, negative	Trade-off	(Engel *et al*. 2005)
4	Marine protected area development	Regulation of algae growth	Tourism	Yes	Similar	Unidirectional, positive	Synergy	(Hughes *et al*. 2005)
5	Dry spells	C sequestration/ soil organic matter	Crop yield	No	–	Bidirectional, positive	Synergy	(Enfors *et al*. 2008)
5	Pesticide spraying	Wood production	Pest control	No	–	Bidirectional, negative	Trade-off	(Clark *et al*. 1979)
6	Cloud forest land clearing	Moisture retention	Carbon sequestration and tree growth	Yes	Similar	Bidirectional, positive	Synergy	(del-Val *et al*. 2006)

Table 2 Research questions about ecosystem services

Understanding the nature of ecosystem services

- Are there consistent sets of ecosystem services associated with different types of land cover or land use?
- Is the composition of these sets shaped more strongly by social or ecological factors?
- How do different ecosystem services flow across the landscape from where they are produced to where they are used or consumed?
- Are there specific processes that regulate the nature of the relationship between specific ecosystem services?

Managing trade-offs and synergies

- What are the empirical patterns of tradeoffs and synergies among sets of ecosystem services?
- What are the most effective ways to mitigate tradeoffs or enhance synergism of ecosystem services?
- How strong are the relationships between ecosystem services and how does the strength of the relationship change with time, management, and across scales?

Understanding regulating services and regime shifts

- How do regulating services affect the dynamics of ecosystem services over time?
- What are the shifts in ecosystem services that occur during regime shifts? How abrupt are these shifts?
- How does variability of ecosystem service provision change with declines in regulating services?
- At what point will incremental change in use of ecosystem services or ecosystem management lead to regime shifts in the provision of ecosystem services?

tem services, potentially producing regime shifts through the feedbacks among provision of ecosystem services. For instance, in cloud forests in Chile, maintaining the forest has an impact on carbon sequestration (regulating ecosystem service) (Fig. 2, Sector 6). The persistence of trees helps retain the moisture found in fog (regulating ecosystem service). In turn, increased moisture retention improves tree growth, further enhancing carbon sequestration (Dawson 1998; del-Val *et al.* 2006). This relationship means that moisture intercepted from fog by vegetation allows the vegetation to persist despite low precipitation. However, without large enough leaf area to intercept fog there is insufficient moisture capture to establish vegetation. Clearing of vegetation can thus result in a regime shift to a savanna or shrubland (Dawson 1998; del-Val *et al.* 2006). Thus, cutting the forests directly reduces carbon sequestration by reducing the tree biomass available to store carbon, but it also reduces moisture retention, which reduces the growth of remaining trees, further reducing carbon sequestration. Our review showed that such interactions frequently involve at least one regulation ecosystem service, echoing the finding that the best indicators of resilience are slowly-changing variables, which may often be regulating ecosystem services (Bennett *et al.* 2005).

Despite their apparent importance, interactions among ecosystem services, particularly those involving regulating services have generally been underappreciated; ecological management and monitoring have focused on provisioning or cultural services (Carpenter *et al.* 2006b). While there has been substantial ecological research on some regulating services such as pollination and carbon sequestration, these services' role in ensuring the reliability of other ecosystem services has not been systematically assessed. However, many examples illustrate that when investments are made to secure regulating services, provisioning and cultural services also improve [e.g. conservation tillage improving erosion control (Pimentel *et al.* 1995), forest patches enhancing pollination and pest control (Ricketts *et al.* 2008), or increasing soil biodiversity to increase nutrient availability (Altieri 1999)]. On the other hand, investing in improving provisioning services seldom automatically increases regulating services, and in many cases appears to lead to declines [e.g. many techniques for improving agricultural yield have led to declines in other ecosystem services (Millennium Ecosystem Assessment 2005)].

Moreover, we propose that declines in regulating ecosystem services can result in declines in ecosystem resilience, even when they do not substantially reduce the levels of other ecosystem services. For example, coral reefs that have been heavily fished may preserve many ecosystem services such as recreation opportunities, even as they lose the ecosystem services that regulate algae levels, making those reefs much less resilient to switching to an algae dominated regime (Hughes *et al.* 2007). The risk of rapid changes in ecosystems, or ecosystem regime shifts is determined by the ecosystem's resilience, its capacity to maintain its structure and functions despite pressure to the system (Scheffer *et al.* 2001). What confers resilience on a system is still largely unknown; however, the ecological dynamics behind dramatic shifts in ecosystem services are often defined by both internal dynamics and external forces (Scheffer *et al.* 2001; Folke *et al.* 2004). Changes in the internal variables that define a regime often are slower than other system dynamics and are referred to as 'slow variables' (Scheffer & Carpenter 2003). Our review suggests that these slow variables usually are related to regulating ecosystem services, and that the strength of regulating services can attenuate the impact of shocks on ecosystems. This is illustrated in the well-known dynamics of coral reef shifts to algae dominated reefs where the regulating service of algae eating declines dramatically before the actually shift happens (Nyström *et al.* 2000; Hughes *et al.* 2007), or in freshwater eutrophication after the soil's capacity to regulate phosphorus loss by sorption is exceeded (Heckrath *et al.* 1995).

Critical research in this area will focus on whether and how regime shifts are related to interactions among ecosystem services as well as how regime shifts themselves affect provision of other ecosystem services. An important aspect of this research is understanding the point at which incremental change in ecosystems or use of ecosystem services finally crosses a threshold that leads to a regime shift, and the role that regulating services play in determining the location of this threshold.

CONCLUSIONS

The literature suggests at least three reasons to be concerned with the relationships among ecosystem services: (1) trade-offs among services can create unwanted declines in some ecosystem services when management focuses on only one at a time (Millennium Ecosystem Assessment 2005; Diaz & Rosenberg 2008); (2) it appears that we may be able to alter these trade-offs by focusing on the ecosystem processes that link services (Pretty *et al.* 2006); and (3) ignoring dynamics may increase the risk of regime shifts in which sudden, unexpected, and often unwanted changes in ecosystem services are experienced (Gordon *et al.* 2008).

This, along with the three propositions, suggests a variety of emerging questions that ecosystem service research should address to improve our understanding of the relationships among ecosystem services and our management of the multiple services provided by landscapes (Table 2). Critical areas of research in ecosystem services include studies that identify common sets of correlated ecosystem services and the situations (landscapes and management regimes) in which they typically occur. Once such bundles have been identified, research to understand the mechanisms behind their grouping (e.g. are the services responding to the same driver or are they interacting) can help us better manage the relationships among ecosystem services, including actually reducing tradeoffs and creating synergies in addition to simply avoiding or taking advantage of them where they already exist. These studies will need to explicitly examine the processes that link services. Finally, we suspect that regulating ecosystem services play a critical role in determining the long-term persistence of sets of ecosystem services. Unpacking the role of regulating ecosystem services in regime shifts and other unanticipated ecosystem changes is a key next step for ecosystem services research.

Ecologists are challenged to guide people to manage ecosystems to produce reliable supplies of many different ecosystem services. Doing this requires that ecologists better understand the dynamics of multiple ecosystem services and develop general rules about the relationships among ecosystem services. Research that quantifies the provision of multiple services and the trade-offs and synergies among them and examines the ecosystem processes that link services will lead to a better understanding of how the relationships among ecosystem services can change over time and space. Such understanding may enable manipulation of systems to decrease tradeoffs, enhance synergisms, and promote resilience and sustainable use of ecosystem services.

SIDE BAR: DEFINITIONS

Many key terms in ecosystem service research are defined differently by different users or, often not defined at all. Here, we provide definitions for some of these terms as we use them in this paper.

Ecosystem services

The 'benefits' that people obtain from ecosystems (Millennium Ecosystem Assessment 2003), including provisioning services, such as food, freshwater, and fibre; cultural services that provide non-material benefits, such as places for recreation and inspiration; and regulating services that provide benefits due to the regulation of ecosystem processes, such as flood control and climate regulation (Daily 1997; Millennium Ecosystem Assessment 2005). This definition of ecosystem services includes services provided by 'wild' ecosystems, such as aesthetic beauty or carbon storage, as well as those provided by intensely managed systems, such as agricultural production or opportunities for recreation.

Driver

A factor, often directly modified by human management, which affects one or more ecosystem services.

Trade-offs

Situations in which one service increases and another one decreases. This may be due to simultaneous response to the same driver or due to true interactions among services. For example, water quality and agricultural production are a well-known trade-off due to differing responses to the addition of nutrients to the agricultural landscape (Carpenter *et al.* 1998).

Synergies

Situations in which both services either increase or decrease. This may be due to simultaneous response to the same driver or due to true interactions among services. For example, a synergistic relationship exists among algal grazing and recreation opportunities in coral reefs within marine protected areas. The protected areas have more fish, which increases algal grazing which protects the coral, and enhances opportunities for recreation (Hughes *et al.* 2007).

Ecosystem service interaction

A situation in which the provision of one service has a direct impact on another service. These can be unidirectional (provision of service A affects the level of provision of service B but not vice versa) or bidirectional (provision of service A affects the level of provision of service B, which affects the provision of service A). They can also be positive (provision of service A increases provision of service B) or negative (provision of service A inhibits provision of service B).

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