CHAPTER FIVE

Tradeoffs and Compatibilities Among Ecosystem Services: Biological, Physical and Economic Drivers of Multifunctionality

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Abstract

Balancing the joint production of multiple ecosystem services, also referred to as the ‘multifunctionality’ of an ecosystem or landscape, requires understanding of the ecological processes that produce and economic processes that evaluate those services. Here,

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we review the ecological tradeoffs and compatibilities among ecosystem processes that influence ecosystem multifunctionality with respect to ecosystem services, including variation in functional strategies, constraints on community assembly and direct effects of the abiotic environment. We then review how different valuation methods may alter the magnitude of tradeoffs and compatibilities in monetary terms. Among communities, functional diversity increases ecosystem multifunctionality, but community-average trait values are emerging as important drivers of ecosystem services with greater potential to produce tradeoffs when compared to functional diversity. However, research that links organismal functional strategies to community assembly rules in real, heterogeneous landscapes demonstrate that predictable tradeoffs among species do not consistently scale up to the community level, necessitating further research on trait-based community assembly in order to develop general predictive models of biotic effects on ecosystem multifunctionality. Abiotic factors are frequently incorporated into mapping assessments of multifunctionality, but the emergent tradeoffs and compatibilities in ecosystem services driven by those factors are rarely assessed, despite a number of studies that have demonstrated their clear importance in ecosystem multifunctionality. Finally, while a variety of valuation methods are used to quantify the joint production of ecosystem services, only provisioning services are typically directly valued and assumed to have fixed correlations with other ecosystem services that can lead to inaccurate valuation, and potentially inappropriate prioritisation, of multiple ecosystem services.

1. INTRODUCTION

Maintaining or creating landscapes that provide many types of ecosystem services has been identified as a critical goal for sustainable natural resource management and conservation (Kremen et al., 2012; Reyers et al., 2012). This concept of 'multifunctional landscapes' has generated renewed interest in ecosystem service research by providing a link between land management practices and the goods and services accrued from natural capital (O'Farrell and Anderson, 2010). The focus on multifunctional landscapes closely parallels recent advances in biodiversity–ecosystem function research (chapter "Towards an integration of biodiversity–ecosystem functioning and food web theory to evaluate relationships between multiple ecosystem services" by Hines et al., this issue), where the focus has begun to shift from single ecosystem functions (e.g. primary productivity) to many ecosystem functions simultaneously (i.e. 'ecosystem multifunctionality'; Hector and Bagchi, 2007; Zavaleta et al., 2010). Basic ecosystem *processes and structures* such as biogeochemical cycling, habitat creation, productivity and natural aesthetics can be conceptualised as ecosystem *functions* that benefit humans which, based on human values, constitute ecosystem *services* (de Groot et al., 2002; chapter "10 Years later: Revisiting priorities for science and society a decade after the millennium ecosystem assessment" by Mulder et al., this issue). Thus, an understanding of the biological and physical drivers of multiple simultaneous ecosystem functions can provide valuable insights into effective management for multiple ecosystem services. Recent research has begun to bridge the gap between drivers of basic ecological processes and their effects on ecosystem multifunctionality, in terms of both ecological functions and the services accrued from them, at a landscape scale (Lavorel et al., 2011; Pasari et al., 2013). Furthermore, methods for estimating the joint economic values of ecosystem services are being developed in order to link ecological processes to human well-being (The Natural Capital Project, 2015), a critical link for sustainable management practices.

Perhaps one of the most fundamental principles spanning ecology and economics is that tradeoffs (e.g. resource use and efficiency or allocation strategies of organisms, opportunity costs in economics), prohibit the stability of 'optimal' strategies across all sets of conditions. It should therefore be no surprise that management strategies for achieving multifunctionality have begun to focus on finding ways to avoid or mitigate underlying ecological tradeoffs as much as possible (Bennett et al., 2009; Rodríguez-Loinaz et al., 2015). Maintaining high biodiversity is one potential solution to minimising tradeoffs, but biodiversity is not a panacea. In a study of grassland plant communities varying in species richness, Zavaleta et al. (2010) found that the levels of biodiversity necessary to sustain just a handful of ecosystem processes at moderate levels could rapidly exceed the available diversity of the regional species pool. Limits on available biodiversity suggest that multifunctionality is in many cases most likely to be achieved across heterogeneous landscapes rather than within a single patch or ecological community type. Thus, to understand how to minimise tradeoffs within a patch or community, it is also crucial that we understand how variation in the physical environment and management practices influence the distribution of biodiversity across heterogeneous landscapes (Lavorel and Grigulis, 2012; Lavorel et al., 2011).

Beyond the generation of ecosystem services derived from ecosystem functions, the values placed on those services through market and other forces can alter their perceived relative importance. How ecosystem services are valued can alter the perception of multifunctionality, depending upon how ecosystem service levels and their values are related. For example, some ecosystem services are relatively insensitive to variation in demand

(Andersson et al., 2015), and values of others are not necessarily linearly related to supply. Value functions are also strongly influenced by the scale at which benefits of ecosystem services are accrued and valued (e.g. single landowner, state or global). Thus, human perception of the ecological tradeoffs that shape ecosystem multifunctionality can be strongly modulated by how, and at what scale, ecosystem services are perceived.

Here, we review the ecological tradeoffs and compatibilities that drive covariation among ecosystem functions and associated ecosystem services, and the economic methods used to value those services (Fig. 1). Much of the focus is on terrestrial ecosystems and associated plant communities, primarily because these are the best understood systems at this time. We begin by reviewing the effects of ecological communities—including both the effects of biodiversity as well as the functional characteristics of dominant species—on ecosystem multifunctionality. We then review the indirect effects of the physical environment and management (e.g. climate, soils, biomass removal) on ecosystem multifunctionality via constraints on community composition, as well as the direct effects of the physical environment. Finally, we assess how different economic valuation methods can be used to assess multiple ecosystem services simultaneously, and their ability to provide accurate information to guide management.

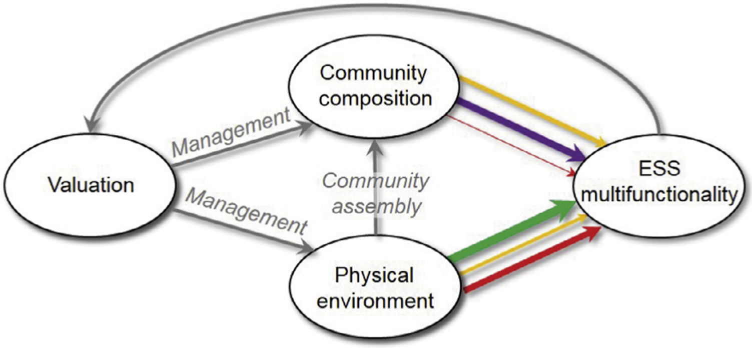

Figure 1 Both the physical environment (e.g. climate, soils) and ecological community composition (e.g. functional diversity, trait values of dominant species) can directly influence levels of different types of ecosystem services (ESS), represented by arrow widths and colours, respectively. Grey arrows represent processes that indirectly influence ESS levels: the physical environment can indirectly drive ESS levels by influencing community assembly, and economic valuation of ESS can feed back to influence all of these processes via management actions. Tradeoffs and compatibilities among ESS and their underlying drivers at each of these steps determine the degree of multifunctionality of ESS.

2. BIOLOGICAL DRIVERS OF MULTIFUNCTIONALITY

Species loss is one of the biggest environmental issues facing humanity today, with current extinction rates estimated to be occurring at three to four times background extinction rates (Barnosky et al., 2011). Species loss impairs ecosystem resilience, which can have profound impacts on ecosystem functioning and ecosystem services (Chapin et al., 2000). Furthermore, the importance of diversity to multifunctionality increases as more functions (or ecosystem services) are considered, a trend that is consistent throughout aquatic and terrestrial ecosystems (Lefcheck et al., 2015). Thus, it is essential to understand the mechanisms by which biodiversity promotes multifunctionality so that key patches or 'hot spots' can be identified and conserved.

Multifunctionality can be quantified in several ways, particularly as it relates to biodiversity. Byrnes et al. (2014) identified four primary approaches, including (1) quantifying multiple ecosystem functions separately, (2) the effects of different species on different functions, (3) the average levels of multiple functions and (4) the number of functions that exceed a critical threshold. They concluded that threshold approaches are likely to be most effective in fully describing variation in multifunctionality, though the case studies covered in this review use a variety of methods for quantifying multifunctionality that depend upon the specific questions being addressed in the study or study-author preference.

2.1 Effects of Taxonomic Diversity on Multifunctionality

Taxonomic diversity refers to the number and relative abundance of species within a community. The linkages between taxonomic diversity and ecosystem functioning are well documented, with overwhelming evidence that increasing the number of species in a community yields benefits ranging from productivity to stability. It is not surprising then, that species richness promotes multifunctionality as well as the levels of single functions. The key distinction is that while the positive effects of species richness on single functions tend to saturate at moderate to high levels of richness, this saturation rarely occurs when considering many functions simultaneously.

The majority of multifunctionality studies have used plant communities as their model system, with generally consistent results; at Cedar Creek Ecosystem Science Reserve, more diverse communities exhibited greater productivity, forage quality and resistance to invaders, and the minimum number of species required to surpass critical thresholds in these ecosystem functions consistently increased with the number of functions considered (Zavaleta et al., 2010). This result was extended for grasslands, more generally, by the work of Isbell et al. (2011) that found additional diversity was necessary when accounting for spatial and temporal environmental variation, relative to static levels of multifunctionality within homogeneous patches. In boreal and temperate forests of Sweden, biomass production was 54% greater with five tree species than only one tree species, and different species were most strongly related to different functions, indicating that monocultures will lead to reduced levels of multifunctionality (Gamfeldt et al., 2013). Across drylands globally, species richness contributes positively and significantly to multifunctionality when considering a variety of functions related to carbon cycling and nutrient retention (Maestre et al., 2012). In a meta-analysis of agricultural ecosystems, within crop diversification (polycultures) promoted yield and biocontrol simultaneously, suggesting synergistic outcomes at both the plant and plot levels (Iverson et al., 2014). In bacterial systems, linkages between species richness and multifunctionality of biofilms have found that the likelihood of sustaining multiple ecosystem functions (production of a suite of extracellular enzymes) decreased with decreasing species richness (Peter et al., 2011). There are exceptions to the general pattern, however. Zavaleta et al. (2010) found that plant N is maximised in monocultures, whereas invasion resistance is maximised with high species richness.

The diversity of trophic and mutualistic interactions within communities can also influence multifunctionality. Hensel and Silliman (2013) found that multifunctionality increased when there was a diverse consumer assemblage consisting of snails, crabs and fungi, and consequences of species loss depended on how many functions were examined. In agricultural ecosystems, increasing the richness of a suite of natural enemies reduced the density of a widespread group of agricultural pests, increasing yield (Cardinale et al., 2003). Mutualistic interactions between arbuscular mycorrhizas and plants lead to improved soil stability, abiotic stress tolerance and carbon storage in ways that plants cannot achieve alone (Gianinazzi et al., 2010). Wagg et al. (2014) manipulated the biodiversity of soil microbial communities and found that biodiversity loss impairs multiple ecosystem functions such as C sequestration, litter decomposition and aboveground productivity, likely due to disruption of plant–microbe interactions. However, mutualisms can also produce tradeoffs among ecosystem functions, depending on management goals; fescue (*Festuca*) species are commonly infected with endophytic fungi, which enhance drought tolerance but decrease forage quality for insect and ungulate herbivores through the production of toxins (Aiken and Strickland, 2013).

Genetic diversity within species can also influence multifunctionality. Increasing the genotypic diversity of *Solidago altissima* results in higher arthropod diversity, community structure and aboveground productivity (Crutsinger et al., 2006). Genetic differences can even produce ecosystem-level afterlife effects; immobilisation of nitrogen and phosphorous was greater in litter representing multiple cottonwood (*Populus*) genotypes rather than single genotype mixtures (Schweitzer et al., 2005). Further efforts to explore plasticity and genetic diversity as drivers of ecosystem multifunctionality will yield valuable insight for population and landscape level species distribution models, as well as help to maximise restoration benefits in a changing world.

Whether interspecific or intraspecific diversity is considered, using species or genotypes as the units of interest can limit the development of predictive models of ecosystem multifunctionality. In the example of forest trees in Sweden discussed above, Gamfeldt et al. (2013) identified differences in how individual tree species influenced ecosystem functions, and in turn how their combined effects at the community level drove tradeoffs and compatibilities among those functions (Fig. 2). This is an excellent example of how tradeoffs among species can be used to predict ecosystem multifunctionality, but unfortunately the results are not easily translated to other systems with different species. Unless tradeoffs and compatibilities among ecosystem functions are identical across systems, our ability to predict such relationships and resulting multifunctionality in other systems is limited when using species or genotypes as the common denominators.

2.2 Effects of Functional Composition on Multifunctionality

Functional traits can provide the necessary links among species and ecosystems that are not always apparent when considering only taxonomic approaches to community composition (McGill et al., 2006). Functional traits are organismal characteristics that respond to and influence the abiotic and biotic environment (Lavorel and Garnier, 2002). Importantly, functional traits are generally comparable across species and communities, regardless of whether there is overlap in species composition across those communities.

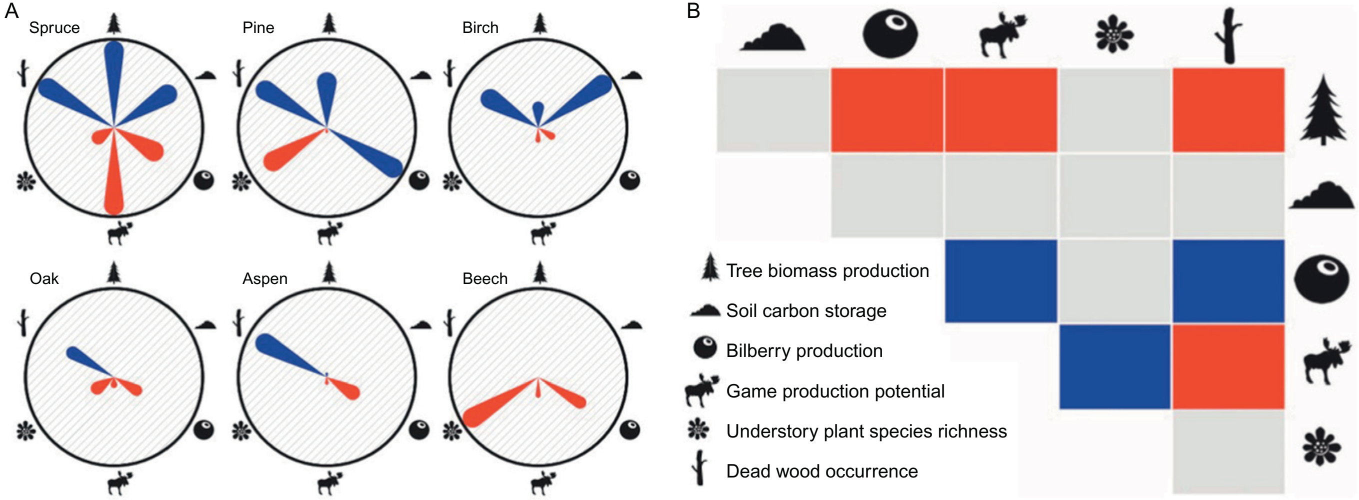

Figure 2 Tradeoffs and compatibilities among multiple ESS in forest ecosystems in Sweden. Tree species impacts on different ESS are presented in (A), where blue (black in the print version) and red (grey in the print version) lobes indicate positive and negative effects, respectively. The net effects of those species across communities in which they vary in their relative abundances produce tradeoffs (red; grey in the print version) and compatibilities (blue; black in the print version) among ESS at the ecosystem level (B), despite generally positive effects of tree diversity on individual ESS (not shown). *Reproduced from Gamfeldt et al. (2013).*

The distribution of functional trait values within communities can also provide a multifaceted and generally superior approach to quantifying the potential effects of communities on ecosystem functions relative to taxonomic measures of diversity (Villeger et al., 2008). Both the diversity and community-average values of functional traits have been shown to influence ecosystem multifunctionality, and the specific functional drivers of different services may provide general predictions for tradeoffs and compatibilities.

2.2.1 Functional Diversity

Evidence for the importance of functional (rather than taxonomic) diversity in driving ecosystem multifunctionality has recently begun to accumulate. In synthetic herbaceous plant communities, Mouillot et al. (2011) found that functional divergence (which can be interpreted as the functional uniqueness of a community; Villeger et al., 2008) was the strongest predictor of multifunctionality (with a positive effect) related to four different ecosystem functions, whereas taxonomic diversity was rarely a significant predictor. The importance of functional diversity for a variety of ecosystem services holds for natural communities across heterogeneous landscapes as well (Laliberte and Tylianakis, 2012; Lavorel et al., 2011; Valencia et al., 2015). The importance of functional diversity for multifunctionality also extends to animal assemblages, where a meta-analysis has shown that across five types of animal groups, functional diversity has a stronger positive effect on a variety of ecosystem services, and hence multifunctionality, than does taxonomic diversity (Gagic et al., 2015).

2.2.2 Community-Average Trait Values

Many ecosystem services appear to be better explained by the central tendency of functional trait distributions, typically quantified as community-average trait values, than functional diversity *per se*. Grime (1998) proposed what he called the ‘biomass-ratio hypothesis’, which states that species’ effects on ecosystem processes are proportional to their relative contributions to total biomass; thus, most ecosystem processes can be explained by the traits of dominant species, or more generally by the biomass-weighted average trait values of communities. This theory has garnered empirical support in terrestrial plant ecosystems. Mokany et al. (2008) evaluated plant leaf, root and litter traits within a grassland and found that community-average trait values best explained the variation in five of the eight ecosystem functions examined, though multifunctionality was not assessed. A variety of studies have demonstrated that both community-average trait values and functional diversity contribute to different ecosystem services (Butterfield and Suding, 2013; Klumpp and Sousanna, 2009; Lavorel et al., 2011; Mouillot et al., 2011). Body size of bees and beetles has also been found to contribute the most to a variety of ecosystem functions, including dung burial and pollen deposition, but at a cost to likelihood of local extinction (Larsen et al., 2005).

Ecosystem functions driven by community-average trait values have the greatest potential for strong interactions. Lavorel et al. (2011) found a tradeoff between fodder quantity and quality in a pastoral landscape, driven by positive and negative effects, respectively, of plant height. In contrast, Laliberte and Tylianakis (2012) found a positive relationship between primary production and soil carbon storage due to a positive effect of specific leaf area on both functions. In a review of ecosystem functioning studies, de Bello et al (2010) suggested that bundles of traits, or 'trait-service clusters', combine and interact to determine the levels of different ecosystem services, and that identifying these clusters at different scales could help to predict and manage for variation in multifunctionality within and across ecosystems.

Most studies find that some ecosystem functions are driven by functional diversity and others by community-average trait values. Such combinations present opportunities for high multifunctionality if the underlying mechanisms are well-understood (Fig. 3). Because functional diversity and community-average trait values (the spread and central tendency of trait distributions, respectively) are mathematically independent, species combinations could be selected through management that simultaneously maximise ecosystem functions driven by diversity and mass-ratio mechanisms.

3. COMMUNITY ASSEMBLY AND MULTIFUNCTIONALITY

Experiments with synthetic communities in homogeneous environments have laid the foundation for our understanding of how biodiversity influences ecosystem functioning (Hooper et al., 2005). Over the past decade, biodiversity–ecosystem functioning research has begun moving into the 'real world', and the focus on multifunctionality is one indicator of this movement (Hines et al., this issue). Studies are beginning to demonstrate that realistic assemblages generate distinctly different patterns of multifunctionality than do randomly assembled sets of species (Bracken and Williams, 2013). Mapping the landscape distribution of ecosystem service delivery to identify "hot" and "cold" spots in multifunctionality has also made it clear that the ability of patches to supply ecosystem services is

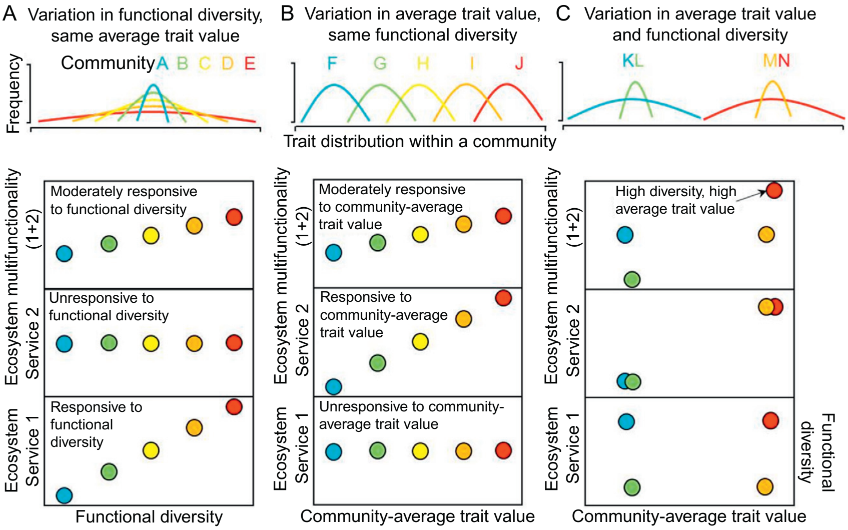

Figure 3 Opportunities for avoiding tradeoffs and maximising multifunctionality of two (or more) ESS driven by diversity and mass-ratio mechanisms, respectively. (A) Communities A–E have the same community-average trait values, but vary substantially in functional diversity, here represented as the breadth of trait values within a community. Ecosystem service #1 is positively related to this variation in functional diversity across communities, whereas ecosystem service #2 is unrelated to functional diversity, resulting in an overall weak response of ecosystem service multifunctionality (combination of #1 and #2) to variation in functional diversity. (B) Communities F–J vary in their average trait values, but are identical with respect to functional diversity. Ecosystem service #2 is positively related to this variation in average trait values across communities, whereas ecosystem service #2 is unrelated to community-average trait values, resulting in an overall weak response of ecosystem service multifunctionality to variation in community-average trait values. (C) If management can be used to preferentially select for certain species, in this example a community with a high average trait value and high functional diversity (community N) would result in high multifunctionality, despite the component ecosystem services being driven by different mechanisms.

constrained in part by the physical environment and management (Pagella and Sinclair, 2014). Non-random species assemblages and exogenous constraints on ecosystem multifunctionality in part reflect community assembly processes—the filtering of species into local assemblages via dispersal, abiotic and management factors (e.g. frost, aridity, grazing) and biotic interactions (e.g. competition and facilitation). The composition and diversity of ecological communities, and their follow-on effects on multifunctionality as described in the previous section, modulate the effects of the abiotic environment and management actions on multifunctionality. Precisely how communities translate variation in the environment and management into multifunctionality depends upon the nature of ecological tradeoffs associated with community assembly.

Indirect effects of the abiotic environment or management on multifunctionality can be predicted through a functional response–effect framework (Lavorel and Garnier, 2002). Response traits are those that determine how the abundance or biomass of a species changes in response to specific disturbances or environmental variation in time or space. In turn, effect traits drive variation in ecosystem functions. Whether or how response and effect traits are related to one another (or if those traits are one and the same) can be used to predict how ecological communities modulate environmental signals in ecosystem functioning (Hevia et al., this issue; Suding et al., 2008).

3.1 Functional Responses to Variation in the Environment and Management

3.1.1 Diversity Responses

A substantial body of evidence suggests that diversity promotes multifunctionality. Understanding the drivers of that diversity can therefore be used to develop predictive models of multifunctionality by providing the 'response' side of the functional response–effect model of community effects on ecosystem functioning (Suding et al., 2008). In general, diversity can be expected to increase in more benign (i.e. nutrient-rich, not abiotically limiting) environments and decrease in more severe environments, referred to as the 'stress dominance hypothesis' (Coyle et al., 2014). At the scale of the Western Hemisphere, Swenson et al. (2012) found that the diversity of several key plant functional traits (height, leaf %N, seed mass, specific leaf area and wood density) generally increased towards the tropics and lower elevations, and increased with increasing temperature and precipitation. Hulshof et al. (2013) found similar patterns of increasing diversity of specific leaf area at lower elevations across several regional gradients. Using a multidimensional approach to functional diversity, Butterfield (2015) also found support for lower functional diversity of woody plants in dry and cold environments across the southwest USA, though at least one dimension of functional diversity also declined at the wet and warm ends of the gradients. Coyle et al. (2014), however, found no consistent trends in forest tree functional diversity across more modest environmental gradients of the eastern USA. At a landscape scale, Cornwell and Ackerly (2009) found an increase in the diversity of several functional traits (leaf area per sapwood area, wood density and height) with increasing soil water availability but a decrease in leaf nitrogen diversity. In short, while not universal, functional diversity tends to be greater in more benign than severe environments, which in theory should result in greater potential for ecosystem multifunctionality in more benign environments. These examples suggest that the increase in functional diversity (and hence multifunctionality) with decreasing environmental severity is more likely to play out at broad spatial scales, though there is potential for predictable landscape-scale variation in diversity and associated ecosystem services if fine-scale environmental gradients are sufficiently steep.

An exception to the stress dominance hypothesis outlined above can occur when competition plays an important role in community assembly. Specifically, competition often increases in importance in benign and late-successional environments, resulting in the exclusion of competitively inferior species and a reduction in diversity. This decline in diversity can also result in a reduction in multifunctionality. For example, in the Machair grasslands of Scotland (Pakeman, 2011), cessation of historical land management practices such as grazing and hay-making have resulted in lower functional diversity and reduced multifunctionality related to a variety of functions. Maintaining diversity through moderate biomass removal or other forms of disturbance is consistent with the intermediate disturbance hypothesis (Connell, 1978; Fig. 4). Multifunctionality, as driven by diversity effects of communities, may therefore only be expected to be high in benign environments if historical or natural disturbance regimes are in place.

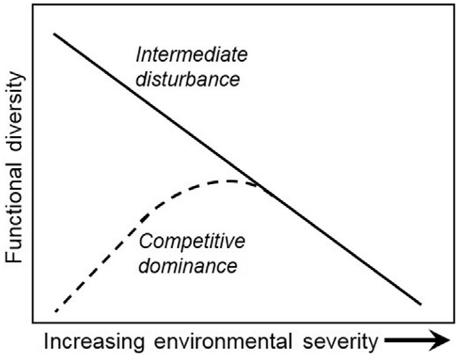

Figure 4 Hypothetical relationship between environmental severity and functional diversity. Increasing competitive intensity with declining environmental severity can result in a reduction of functional diversity (and hence ESS multifunctionality) unless disturbances of intermediate intensity and frequency can reduce competitive exclusion.

3.1.2 Community-Average Trait Responses

Much as diversity can vary predictably with the environment, so too can community-average trait values. Tradeoffs among different functional strategies can provide a framework for predicting community-level tradeoffs in the ecosystem services that they influence, and the environmental-dependence of those tradeoffs. Perhaps the most pervasive tradeoff is between resource use efficiency and potential growth rate (e.g. Brown et al., 2004; Grime et al., 1997), which in turn can have a strong environmental- and successional-dependence. For example, in abandoned agricultural fields, Garnier et al. (2004) found that as functional strategies shifted from opportunistic to conservative with increasing time since abandonment, productivity declined but soil carbon content and fertility increased, resulting in moderate multifunctionality across the successional time series. Just as with the example of disturbance being necessary to sustain diversity-driven multifunctionality in Machair grasslands discussed above, maintaining patches in different stages of succession through natural (or historical) disturbance regimes may be a way to avoid tradeoffs among ecosystem functions associated with community-average values of different traits within a heterogeneous landscape.

In reality, few organismal tradeoffs are truly unavoidable (Westoby et al., 2002) and typically manifest as broad 'manifolds' that encapsulate a great variety of functional strategies among species (Wright et al., 2004). Tradeoffs evident among species can change dramatically when scaled up to community-average trait values across environmental gradients, thus it may be difficult to predict tradeoffs among ecosystem functions driven by different traits when assessing functional tradeoffs across species, rather than across communities. Interestingly, correlations among traits tend to be stronger at the community-average level than at the species level (i.e. stronger across communities than across species; Ackerly and Cornwell, 2007; Kooyman et al., 2010), indicating coordinated ecological selection on multiple traits through the course of community assembly (Fig. 5). Thus, relatively weak tradeoffs apparent among species may tend to be more consistent, and qualitatively different, at the community level. Trait relationships can also vary substantially along different environmental gradients (Fonseca et al., 2000). Thus, while an understanding of ecological tradeoffs at the organismal or interspecific level can be informative, a better understanding of how (or if) those tradeoffs scale up to community-average trait values along environmental gradients is necessary to understand tradeoffs among ecosystem functions and the resultant degree of multifunctionality.

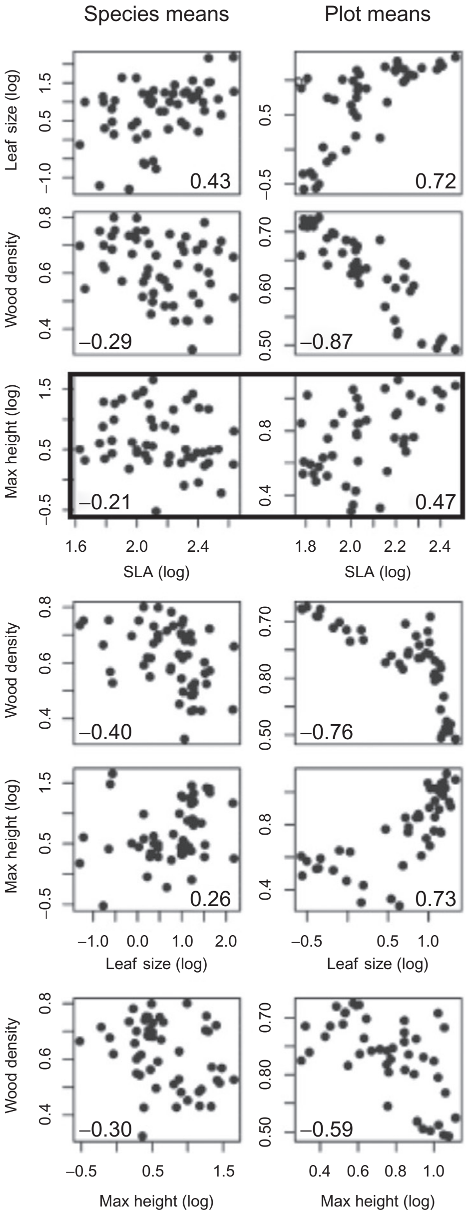

Figure 5 Examples of differences in functional trait relationships at the species versus community levels. The scatter plots represent relationships among species average functional traits (left) and community-average functional traits (right) of woody plants in coastal California (Ackerly and Cornwell, 2007). Correlation coefficients are reported in lower left or right corners. In most cases, relationships are stronger across communities than across species. Relationships can even change qualitatively, for example, the switch from a negative to a positive relationship between specific leaf area (SLA) and height when shifting from the species to community levels (highlighted by box). *Adapted from Ackerly and Cornwell (2007).*

3.2 Community Assembly Effects on Multifunctionality

The role of ecological communities in mediating environmental and management effects on ecosystem multifunctionality has only been studied directly in a handful of cases. However, these studies clearly illustrate the challenges in developing general response–effect models as they relate to ecosystem multifunctionality. Perhaps the best understood system in this regard is the Lautaret research area in the French Alps, a subalpine landscape varying in elevation, soil properties and land use (Lavorel et al., 2011). Plant community functional composition and diversity, as well as multiple ecosystem services (agronomic value, cultural value, pollination value, soil carbon stock), have been measured and mapped across this heterogeneous landscape. Lavorel et al. (2011) found that nearly all aspects of plant community functional composition and diversity responded to variation in land use type and the physical environment, and in turn that management, physical environment and functional composition of plant communities influenced ecosystem service delivery. It was because many of the plant traits that drove different ecosystem services were relatively independent and responded differently to the environment and land use that a wide range of multifunctionality levels were found. Much of this independence among ecosystem services was driven by different trait-based means of achieving high agronomic value (larger plants or more nutrient-rich leaves), which represent independent axes of functional differentiation.

Carbon storage and forage production are two ecosystem services that are commonly measured in grassland systems, and that illustrate the difficulty in scaling fundamental ecological tradeoffs to predictions of ecosystem multifunctionality (Lavorel and Grigulis, 2012; Table 1). In grassland mesocosms, Klumpp and Soussana (2009) found that greater diversity of specific leaf area values within a community resulted in higher aboveground productivity (an ecosystem function that supports the service of forage production), whereas communities with greater average root density resulted in greater soil carbon (the function leading to carbon storage). Butterfield and Suding (2013) found that greater community-average height resulted in higher aboveground productivity, and that greater diversity of root density resulted in higher soil carbon. In both of these cases, multifunctionality was moderate due to different, independent drivers of the two ecosystem services (as with Lavorel et al., 2011);

Table 1 Summary of Functional Drivers of Soil Carbon and Forage Production in Several Grassland Ecosystems, and the Consequent Multifunctionality of Those ESS

Study	Soil Carbon	Forage Production	Multifunctionality
Klumpp and Soussana (2009)	CWM[a] root density	FD[b] specific leaf area	Moderate
Lavorel et al. (2011)	CWM leaf dry matter and *P* content	CWM height and leaf N content	Moderate
Laliberte and Tylianakis (2012)	CWM specific leaf area	CWM specific leaf area	High
Butterfield and Suding (2013)	FD root density	CWM height	Moderate

[a] CWM—community-weighted mean.
[b] FD—functional diversity.

furthermore, functional diversity and mass-ratio effects were important for different ecosystem functions in these two cases. In contrast, Laliberte and Tylianakis (2012) found an increase in both aboveground productivity and soil carbon through time with increasing agricultural inputs, due in part to a positive response of community-average specific leaf area to increasing soil resource availability that in turn had a positive effect on productivity and soil carbon. These case studies illustrate just some of the observed covariation in two ecosystem services that *a priori* might be expected to be tightly linked (associated with two pools of the same element cycle), due in part to the importance of environmental, management and species pool context-dependence. Some of this variability in multifunctionality can also be attributed to the relative importance of functional diversity versus mass-ratio effects, which are not expected to be tightly linked, though even traits that are well-understood at the species level can demonstrate surprising patterns when aggregated to the community level (Lavorel and Grigulis, 2012). Until we have a better understanding of how ecological tradeoffs at the species level scale up to determine community-level patterns of functional composition and diversity (Ackerly and Cornwell, 2007; Enquist et al., 2015), general models of the responses of ecological communities to environmental variation and subsequent effects on ecosystem multifunctionality will remain elusive.

3.3 Projecting Community Assembly Models and Multifunctionality

Despite the limitations in our understanding, as outlined above, one of the objectives of response–effect community assembly models is to accurately predict both temporal changes spatial environmental variation in ecosystem multifunctionality. Using a space-for-time substitution, Valencia et al. (2015) demonstrated that resilience of multifunctionality to increasing aridity projected to occur in the near future in Mediterranean ecosystems should increase with functional diversity and a strong component of post-fire sprouters (a community-average trait effect). Using a different approach, Moor et al. (2015) used species distribution models to project changes in community-average trait values under climate change in central Sweden, finding mixed projections for changes in several ecosystem services and thus moderate multifunctionality. The latter approach did not require a mechanistic understanding of how traits respond to environmental change, but rather used species-specific responses to environmental variation to predict future community composition. This approach also differed from most current ecosystem service mapping strategies, which do not use species-specific responses (references in Pagella and Sinclair, 2014).

A mechanistic, response–effect trait-based framework for predicting climate change impacts has been applied to the Lautaret system. By integrating projected effects of climate change on plant community functional composition based on current mechanistic relationships, as well as the expected effects of climate change on management actions, Lamarque et al. (2014) found that the direct effects of climate change on functional composition had a much stronger effect on ecosystem multifunctionality than did management. Furthermore, the set of predominant ecosystem services expected to be supplied at high levels was projected to switch, shifting from a landscape that predominantly supplies high levels of forage and diversity to one with higher levels of soil carbon and fertility. Multifunctionality may therefore remain similar, but the component ecosystem services may change dramatically due to the effects of environmental change on a suite of functional traits.

Lavorel et al. (2015) suggested an extension of the ecosystem services definition to include 'climate adaptation services', or the properties of ecosystems that can buffer losses of ecosystem services under changing conditions or after novel shocks would have value. Using several case studies, they found that vegetation structural diversity, keystone species or functional groups, functional response diversity and landscape connectivity were all important for minimising negative impacts of environmental change on ecosystem service delivery. Thus, incorporating modulatory factors such as landscape connectivity and vegetation structure, in addition to functional diversity and composition effects, may improve our ability to predict ecosystem multifunctionality in a changing climate and undertake effective management actions.

4. DIRECT ABIOTIC AND MANAGEMENT DRIVERS OF MULTIFUNCTIONALITY

The abiotic environment can drive substantial variation in ecosystem functions and services, independent of biotic variation. Díaz et al. (2007) proposed an analytical hierarchy for predicting variation in ecosystem functioning that prioritises abiotic drivers, followed sequentially by community-average trait values, functional diversity and unique species effects. Abiotic factors may be sufficient to explain variation in ecosystem functions if (1) biotic variation has relatively weak effects, or (2) if biotic factors are important but vary consistently with the abiotic environment. While tradeoffs and compatibilities among ecosystem functions and services driven by biotic factors may vary strongly with environmental and biogeographic context, those associated with abiotic drivers may be more predictable. Whether or not management interventions to mitigate tradeoffs among ecosystem functions associated with abiotic drivers can be effective or even possible depends on just how easily abiotic drivers of different ecosystem services can be manipulated.

Despite the acknowledged importance of abiotic factors in influencing multifunctionality (Díaz et al., 2007), studies that directly quantify such effects (primarily of climate and soil) are rare and typically take place in grasslands. For soils in particular, there is a tendency to address multifunctionality by examining the effects of species richness on soil variables as opposed to the effects of soil variables (e.g. bulk density, pH) on multifunctionality (Hooper et al., 2005). However, Maestre et al. (2010) showed that, across an eight site grassland regional gradient in Spain, effects of annual radiation, mean annual temperature and rainfall were the largest contributors to variance explained of ecosystem functions and consequent multifunctionality related to soil enzymatic activity. The individual drivers and their relationship to ecosystem services are unclear as only composite environmental effects are reported in the structural equation modelling approach that was used. Across

224 dryland systems, Maestre et al. (2012) found that mean annual temperature and sand content of soil emerged as the most important abiotic controls of multifunctionality (here, assessed across functions related to C-N-P biogeochemistry). Higher multifunctionality was associated with cooler temperatures and lower sand content, suggesting that soil moisture water is an important arbiter of multifunctionality in drylands.

In a predominantly grassland study in the Central French Alps, Lavorel et al. (2011) showed that using abiotic factors of altitude, radiation, soil water holding capacity, soil nutrient status, in addition to trait-based factors, resulted in a higher proportion of variance explained for multiple ecosystem services. However, the directionality of these relationships is usually not explicit. Both soil carbon stocks and litter decreased with altitude but the response surface varied with management by terracing, mowing or grazing. Plant species diversity increased with soil nitrogen availability, which indirectly alters water holding capacity. Working in Pacific Northwest temperate rainforests, Brandt et al. (2014) examined multifunctionality and biodiversity by explicitly including climate drivers (19 BIOCLIM variables) though the directionality of the relationships between specific climate variables and multifunctionality were not described. Instead climate was collapsed to two principal components and analysed in relation to species richness. The climate variable, after that of biogeographic region, captured most of variation in species richness. The lack of explicit linkage between abiotic factors and ecosystem services in such studies is unfortunately typical; a rigorous quantitative treatment of how each factor influences multifunctionality has not been done.

Tradeoffs are inherent in soil-related physical drivers of multifunctionality. Particularly in agriculture systems there is an interplay between soil and management. For example, a highly fertilised soil can function as a medium for crop production but will not protect ground- and surface water from nitrate pollution (Karlen et al., 2011). Variation in incorporation of carbon into soils (sequestration of soil organic carbon) is related to soil properties and cropping systems (no-till vs. conventional tillage as well as amount, quality and frequency of the crop residues) (Batlle-Bayer et al., 2010; de Moraes Sá et al., 2013). Soil organic carbon accumulation generally increases under high-input cropping regimes, although there is uncertainty as to how far down the soil profile this extends. More generally, switching to no-till systems reverses the process of soil degradation and increases both soil quality and CO_2 uptake by the terrestrial biosphere, thereby enhancing multifunctionality (de Moraes Sá et al., 2013).

The relevance of cropping regime highlights the importance of management in modulating multifunctionality. In a study focusing on soil functioning (infiltration ability, surface stability and nutrient cycling) in relation to drought stress (slope aspect) and goat grazing in semi-arid fields in southeastern Spain, Verwijmeren et al. (2014) showed vegetation cover and soil functioning decrease with higher grazing pressure and drought stress. Sandhu et al. (2010) demonstrate that, across 29 arable fields in New Zealand, among three ecosystem services (biological control of pests, soil formation and the mineralisation of plant nutrients) biological control is significantly higher in organic fields than conventional fields. Total economic value was higher for all three ecosystem services in organic fields, however. Disturbance may also have interactive effects with climate. For example, Kienast et al. (2009) found that, under current land use, the potential of high ecosystem service levels associated with food and raw materials derived from cultivated land and aquaculture—as modulated by abiotic factors of *inter alia* soil stability, irrigation and geomorphology—exhibited a tradeoff with net productivity in precipitation-sensitive drier areas of Europe.

5. ECONOMIC VALUATION OF MULTIPLE ECOSYSTEM SERVICES

The preceding sections outline the roles of the biota and environment in regulating multiple ecosystem services, which ultimately can be valued on a monetary basis to inform policy and management. When put in monetary terms, tradeoffs and compatibilities among different ecosystem services can ideally be used to guide management that will result in the highest combined value of services accrued from an ecosystem. Valuation of ecosystem services is not, however, a straightforward task in many cases, and differences between multifunctionality and monetary value can arise through differences in valuation methods among services. Here, we review a set of valuation methods and their potential for guiding management for multiple ecosystem services, as well as potential biases in estimating the combined value of those services.

Surprisingly, when it comes to the economic valuation of ecosystem services, not all services identified in the Millennium Ecosystem Assessment (2005) are being valued economically. Out of the four categories of ecosystem services (supporting, provisioning, regulating and cultural), supporting services (e.g. nutrient recycling, primary production and soil formation) are almost never valued because they are viewed as a basis for the other three categories of services. Thus, their value is subsumed within the other services. Provisioning services (e.g. food, raw materials and minerals) generally have a clear, well-defined market so there is no need to use other economic methods to identify their value. Both regulating and cultural services have value but often lack markets and thus there is a set of economic methodologies that have been developed to value some of these services.

If ecosystem services secured from the environment are not priced in the market, there are several options available to estimate their value. These methods include, but are not limited to: production functions, stated preference and revealed preference methods (Heal, 2007). While there are economic and non-economic methods to value ecosystem services, this paper will focus only on the effects of using economic methods on the relationship between multifunctionality and valuation, since information gleaned from these methodologies has been the most accessible to policymakers. It should be noted that current work on production functions often incorporates non-economic spatial analysis that will be examined below.

While much effort has been put into incorporating multiple ecosystem services into economic valuation, there is still a dearth of information and case studies to demonstrate how this information can be relayed to policymakers and how that then feeds back to impact the multifunctionality of an ecosystem. Empirical information on the quantitative relationship between land use and ecosystem management and the provision of ecosystem services at the local and regional scale is still scarce and 'to date, there appear to be no examples of complete landscape-scale assessments of the quantity, quality and value of an entire bundle of ecosystem services under alternative management regimes (ICSU et al., 2008)'.

5.1 Production Functions

What is named ecosystem multifunctionality in ecology is the same as a production function or joint production function in economics. Box 1 demonstrates a production function that looks at the multiple ecosystem services that exist on land used for cattle grazing. What is unique about this production function is that it takes into account more than just the standard inputs for cattle grazing, such as water, feed and fertiliser, etc., by incorporating multiple ecosystem services as inputs into the production of cattle.

Multiple services provided by the same ecosystem are considered 'joint products' in economic terms (Fisher et al., 2007). Ecological production functions are mathematical expressions that estimate the effects of changes

BOX 1 Basic Ecological Production Function Example Land Use: Cattle Grazing

1. $h = h(E_1 \ldots E_n, S_{\mathrm{k}})$
2. $h = AE_{\mathrm{j}}{}^{a} S_{\mathrm{k}}{}^{b}$
3. $C^* = C(h, w, S_{\mathrm{k}}) = wA^{-1/a} h^{1/a} S_{\mathrm{k}}{}^{-b/a}$
4. $P = C^*/h$
5. Solve for equilibrium level of cattle harvest, h
6. Take $\mathrm{d}h/\mathrm{d}S_{\mathrm{k}}$ to get the marginal impact of a change in grazing area for different ecosystem services
7. Integrate the change in the price over different harvest levels to get the change in consumer surplus

- h = marketed harvest of cattle
- A = total factor productivity (technology change or efficiency, not a direct input)
- E_{j} = standard inputs for cattle: water, feed, fertiliser, grass, vaccines
- S_{k} = water quality, water quantity, biodiversity, carbon sequestration
- C^* = cost minimising function
- w = unit cost of effort
- P = price equals average cost

The goal in this example is to minimise cost. The result is the marginal impact of a change in cattle grazing habitat and the change in consumer surplus associated with a change in the cattle grazing area. Consumer surplus is the monetary gain obtained by consumers because they are able to purchase a product for a price that is less than the highest price that they would be willing to pay.

in the structure, function and dynamics of an ecosystem on outputs that are directly relevant and useful to decision makers (Environmental Benefits Analysis, 2015). In the example in Box 1, one can evaluate the effect of a change in multiple ecosystem services on the grazing area for cattle.

The production function method recognises that many ecosystem services are used in production as indirect inputs. This approach identifies the physical effects of changes in a biological resource or ecological function on an economic activity and the impact of these changes is then valued in terms of the change in the marketed output of the activity (Barbier, 2007).

Tradeoffs exist when looking at multiple ecosystem services or multifunctionality through the production function method. Utilising spatial econometrics, Simonit and Perrings (2013) show that reforestation within the Panama Canal watershed does not necessarily increase water supply (provisioning service), but does increase carbon sequestration (regulating service) and timber production (provisioning service) during dry periods.

In this system, grassland conversion to natural forest would reduce dry-season flows by 8.4% in the entire watershed. The 4.3% of grasslands capable of providing a potential water flow benefit if reforested could, at the biological steady state yield an additional 3.54 million m^3 to Canal navigation during the dry season, equivalent to US$ 1.56 million in revenue to the Panama Canal Authority in 2009 dollars. Dry-season water flow is not, however, the only ecosystem service provided by the watershed. The authors found that in most areas the value of the hydrological losses due to existing natural forest would be compensated by the value of carbon sequestration at a price of 4 $\text{US\$}\,t^{-1}$ C (where t denotes a metric tonne). The authors also found that conversion to teak plantations would also reduce overall dry-season flow by 11.1%. In fact it would have a negative impact on dry-season flows in all but 142 ha of the area currently under grassland. It would also have a lower carbon storage capacity compared with natural forest. Nevertheless, at 4 $\text{US\$}\,t^{-1}$ C, the carbon sequestered by teak plantations would be sufficient to offset the value of the hydrological losses in 40.9% of grasslands (Simonit and Perrings, 2013).

The choice of forest species and the type of forest management depends on the benefits forests are expected to yield. The species chosen to regulate water supplies will not necessarily be the same as those chosen for timber production, carbon sequestration or habitat provision. The Panama Canal Authority is interested in the regulation of water flows to the Panama Canal, but private landholders in the watershed are typically focused on timber products and/or livestock production. The production function method can help draw out these differences between stakeholders and hopefully increase multifunctionality by having a clearer view of the tradeoffs, if any, being made.

More recently, Simonit et al. (2015) modelled the net effect of ponderosa pine forest thinning across the Salt and Verde River watersheds in Arizona on the reliability and cost of water supply (provisioning service) to the Phoenix metropolitan area. They concluded that the erosional impacts (regulating service) of forest thinning (up to 50% of canopy cover) are unlikely to compromise the reliability of the reservoir system while thinning has the potential to increase annual water supply by 8%. According to TEEB (The Economics of Ecosystems and Biodiversity), erosion prevention is considered a regulating service. Soil erosion is a key factor in the process of land degradation and vegetation cover provides a vital regulating service by preventing soil erosion (TEEB, 2015). This represents an estimated net present value of surface water storage of $104 million, considering both water consumption and hydropower generation. Here, the production function method was able to show that a land use change could continue to provide multiple ecosystem services.

Another method for demonstrating affect of the production function method on multifunctionality has been developed by the Natural Capital Project. The Natural Capital Project is a partnership between Stanford University, The Nature Conservancy, the World Wildlife Fund and the University of Minnesota. The Natural Capital Project has developed a spatially explicit model, InVEST (The Natural Capital Project, 2015), which simulates multifunctionality with respect to ecosystem services. InVEST models are spatially explicit, using maps as information sources and producing maps as outputs. InVEST returns results in either biophysical terms (e.g. tonnes of carbon sequestered) or economic terms (e.g. net present value of that sequestered carbon). InVEST models are based on production functions that define how an ecosystem's structure and function, as currently understood, affect the flows and values of ecosystem services. The models account for both service supply (e.g. living habitats as buffers for storm waves) and the location and activities of people who benefit from services (e.g. location of people and infrastructure potentially affected by coastal storms). InVEST has been taken up widely by natural resource managers and policy makers. The major challenge with InVEST is having sufficient data to input into the system. Without site-specific data, InVEST relies on information from benefits transfer, taking economic values from a particular area and using them in another location, which has been controversial because of its lack of specificity to the particular area being analysed. InVEST continues to be one of the main methods used because it can display multiple ecosystem services in order to identify tradeoffs or compatibilities among services.

5.2 Stated Preference

Stated preference methods can be used to value all ecosystem services. This is frequently broken up into a person's willingness to pay (WTP) or willingness to accept (WTA). Stated preference methods use specifically defined questionnaires to elicit estimates of the WTP or WTA for a particular outcome, which could be a change in the provision of an ecosystem service. WTP is the maximum amount of money an individual is willing to give up to receive an ecosystem service or multiple ecosystem services (multifunctionality). WTA is the minimum amount of money an individual would need to be compensated for foregoing an ecosystem service or multiple ecosystem services (multifunctionality).

There are two categories of stated preference methods: *Contingent valuation methods*, which focus on the valuation of a non-market good (i.e. an ecosystem service not valued in the market) as a whole; and *Choice modelling methods*, which focus on valuing specific attributes of a non-market good.

5.2.1 Contingent Valuation Methods

The contingent valuation method can be used to estimate economic values for multiple ecosystem services. It can be used to estimate both use- and non-use values, and it is the most widely used method for estimating non-use values, which are often provisioning or cultural services. It is also the most controversial of the non-market valuation methods. Non-use value is the value that people assign to economic goods (including public goods such as ecosystem services) even if they never have and never will use it. It is distinguished from use value, which people derive from direct use of the good.

Contingent valuation involves directly asking people, in a survey, how much they would be willing to pay for a specific environmental service. It is more often than not a singular ecosystem service. In some cases, people are asked for the amount of compensation they would be willing to accept to give up a specific environmental service. Contingent valuation is one of the only ways to assign dollar values to non-use values of ecosystem services. However, the fact that contingent valuation is based on asking people questions, as opposed to observing their actual behaviour, is the source of much controversy (Adamowicz et al., 1994). The conceptual, empirical and practical problems associated with developing estimates of economic value on the basis of how people respond to hypothetical questions about market situations are often debated in economics.

Some limitations of the contingent valuation method are based on whether it adequately measures people's willingness to pay for the provision of an ecosystem service (Diamond and Hausman, 1994). Contingent valuation assumes that people understand the ecosystem service in question and will reveal their preferences in the contingent market just as they would in a real market. However, most people are unfamiliar with placing dollar values on ecosystem services. Therefore, they may not have an adequate basis for stating their true value. It is also argued that people place a different value on a good in a hypothetical situation compared to an actual situation (Mitchell and Carson, 2013).

In a WTP survey based in Norway, Bernués et al (2015) looked at three different agricultural scenarios and four ecosystem services. They found very similar results across services, in that they all positively covaried strongly across the alternative agricultural scenarios. Because contingent valuation does not explicitly incorporate tradeoffs and compatibilities among services driven by underlying environmental and biotic constraints, this result might be trivial. Based on such information, contingent valuation is not likely to appropriately value the multifunctionality of ecosystem services and should be used with caution when valuing more than one service.

5.2.2 Choice Modelling Methods

The contingent choice method is similar to contingent valuation, in that it can be used to estimate economic values for virtually any ecosystem service, and can be used to estimate non-use as well as use values. Like the contingent valuation method, people are asked to make choices based on a hypothetical scenario. However, it differs from contingent valuation in that it does not directly ask people to state their values in monetary terms. Instead, values are inferred from the hypothetical choices or tradeoffs that people make. Because contingent choice focuses on tradeoffs among scenarios with different characteristics, it is especially suited to policy decisions where a set of possible actions might result in different impacts on ecosystem services.

Both contingent valuation and choice modelling methods were used to evaluate greenhouse gas regulation, waste treatment (nitrogen leaching), soil retention and scenic views on New Zealand's arable land (Takatsuka et al., 2005). People living in and around Canterbury, where there is most crop farming, were surveyed separately from people in the rest of New Zealand. Using the choice modelling method, which included explicit tradeoffs among services, greenhouse gas emission reduction was the most valuable service in Canterbury, whereas nitrate leaching reduction was most valuable in the rest of the country. Furthermore, the values of ecosystem services were always higher when based on the contingent valuation rather than choice modelling methods, regardless of the policy scenario.

Another study of choice modelling looked at the multifunctionality of agriculture in Northern Europe. Researchers used qualitative (socio-cultural) and quantitative (biophysical and economic) methods to obtain a holistic evaluation of the societal value of fjord and mountainous areas in the Nordic countries (Bernués et al, 2015). A representative sample of the local and general populations were asked to choose their most preferred level of delivery of the ecosystem services under three policy scenarios. The general population considered the production of quality products, the conservation of the agricultural landscapes and the conservation of biodiversity to be of comparable importance. Local people, however, placed a greater value on human-managed agricultural landscapes and to the production of local quality products.

Both of the above studies show that the local and general populations place different values on multiple ecosystem services. Thus, choice modelling may have different results when analysing the multifunctionality of an area and may not be as well suited for incorporating multiple ecosystem services as the production function model.

5.3 Revealed Preference

Revealed preference methods expose estimates of the value of ecosystem services based on how people behave in the face of real choices. The two most common revealed preference methods are the *Hedonic Pricing Method*, which involves examining people's purchasing decisions in markets related to the non-market good in question (provisioning or cultural services); and the *Travel Cost Method*, which involves observing costs incurred in the consumption of the non-market good in question.

5.3.1 Hedonic Pricing Method

The hedonic pricing method is used to estimate economic values for ecosystem services that directly affect market prices. It is most commonly applied to variations in housing prices that reflect the value of local environmental attributes. It can be used to estimate economic benefits or costs associated with environmental quality and environmental amenities. The main idea of the hedonic pricing method is that the price of a marketed good is related to its characteristics, or the services it provides (Garrod and Willis, 1999). The hedonic pricing method is most often used to value environmental amenities that affect the price of residential properties.

A clear example of hedonic pricing can be seen when one wants to value the fertility of soil. Soil fertility is not a good that is bought and sold in a market, so there is no market price. However, farms are bought and sold, and data can be collected on farm prices, the price per hectare of the farmland and the quality of the soil on the farms. Correlating the land price per hectare with the quality of the soil to see how much the fertility of the soil adds to the price of the land indirectly estimates the price for soil fertility or what it adds to the market price of land (Heal, 2000).

Unfortunately, the hedonic pricing method only captures the value of ecosystem services limited to things that are often related to housing or land prices, such as cultural services. In addition, this method will only capture people's willingness to pay for perceived differences in ecosystem services, and their direct consequences. If people are not aware of the linkages between the environmental attribute and benefits to them or their property, the value will not be reflected in home prices. In conclusion, the hedonic pricing method is unlikely to simultaneously capture multiple ecosystem services accurately.

5.3.2 Travel Cost Method

The travel cost method is used to estimate economic use values associated with ecosystems, but most often for sites that are used for recreation, a cultural service. The idea of the travel cost method is that the time and travel cost expenses that people incur to visit a site represent the price of access to the site. Thus, peoples' willingness to pay to visit the site can be estimated based on the number of trips that they make at different travel costs.

Measuring recreational quality (cultural service), and relating recreational quality to other ecosystem services quality can be difficult. The travel cost method is limited in its scope of application because it requires user participation. It cannot be used to (1) assign values to on-site ecosystem services that users of the site do not find valuable, (2) value off-site values supported by the site or (3) measure non-use values. Thus, sites that have unique qualities that are valued by non-users will be undervalued.

5.4 Directions for Improvement

In conclusion, the economic valuation technique that has proven to be the most useful for multifunctionality currently is the production function model, which can encapsulate the spatial aspects of multiple ecosystem services. Economic valuation techniques affect management for multifunctionality through their ability to incorporate multiple ecosystem services into their analyses. By only being able to incorporate a singular ecosystem service, the likelihood that the resulting management technique will have a positive effect on multifunctionality is low.

Without quantitative assessments, and some incentives for landowners to provide them, ecosystem multifunctionality tends to be ignored by those making land use and land management decisions (Nelson et al, 2009). Despite our best efforts to place economic value on multiple ecosystem services, most services are still neglected in land use planning and decision-making. As a consequence, highly productive, multifunctional landscapes continue to be converted into more simple, often single-function land use types, such as croplands, or are turned into wastelands, such as eroded land after clear-cut logging (de Groot et al, 2010).

6. CONCLUSIONS

Determining the net effects of management, and abiotic and biotic factors on multifunctionality is complex. While still at a nascent stage of understanding, a few general principles are beginning to emerge at different levels of organisation. From a strictly biotic perspective, tradeoffs among ecosystem services should tend to be strongest when the underlying biotic drivers are based on mass-ratio mechanisms (i.e. community-average trait values), rather than those driven primarily by functional diversity. Furthermore, ecosystem services that are positively related to diversity should not exhibit consistent tradeoffs with services driven by mass-ratio mechanisms; for example, diverse floral resources can support a diverse array of pollinators, even if all of the associated plant species have very similar, high levels of primary production (i.e. ecosystem services driven by diversity and mass-ratio mechanisms, respectively).

When constraints on community assembly are taken into consideration, it is apparent that many biological tradeoffs that scale up to ecosystem service tradeoffs are dependent upon the composition of regional species pools and environmental context. This context-dependence is illustrated well by the diverse relationships between the composition of rangeland plant communities and two important ecosystem services, forage production and soil carbon storage, outlined above. An understanding of the precise nature of tradeoffs among different regional species pools and environments could ultimately allow for selection of species combinations that minimise ecosystem service tradeoffs. For example, using extensive knowledge of a local species pool and ecosystem, Storkey et al. (2015) were able to simulate combinations of species that could minimise tradeoffs in ecosystem multifunctionality. Using a similar approach across many species pools and environments, and testing the predictions empirically, could help to identify general principles for managing ecological communities for multifunctionality that go beyond maintenance of biodiversity. Critically, however, understanding how tradeoffs at the organismal level—the scale of organisation at which functional strategies are typically studied—scale up to community-level variation in functional composition and diversity is still poorly understood, and represents an important step in the link between fundamental ecological tradeoffs and ecosystem service multifunctionality.

A similar challenge exists for ecosystem service valuation, where variation in socioeconomic factors across different regions can significantly alter the relative values of different ecosystem services, and hence the nature of tradeoffs and multifunctionality, even if the underlying ecological factors and levels of production of those services are the same. Identification of ecosystem service tradeoffs can also depend on the valuation method, which varies substantially among different types of services. 'Bundling' of ecosystem service by associating difficult to valuate services with others that have clearer market values is one solution, but typically assume a rigid structure of tradeoffs and compatibilities among services that may not accurately reflect the environmental, biotic and socioeconomic context of ecosystem service relationships.

Lastly, the abiotic environment plays a strong role in driving multifunctionality, but this role has not been studied as extensively as that of biodiversity and functional composition. Yet the contingencies inherent in biotic regulation of multifunctionality may not be as prevalent in abiotic effects, potentially making the latter more consistent and predictable drivers of multifunctionality. Despite being directly incorporated or implicit in GIS layers used to map ecosystem service hot and coldspots, relationships among abiotic drivers and individual ecosystem services are rarely reported (Pagella and Sinclair, 2014). Without comparable datasets and algorithms for estimating and mapping ecosystem services in different landscapes, it will be difficult to come to general conclusions about the roles of different abiotic drivers of those services. Much as community ecologists are homing in on the functional traits and diversity indices that best predict ecosystem service delivery, settling on similar abiotic indices should be considered at least equally important.

6.1 Integrating Drivers of Multifunctionality

Gaps among disciplines need to be bridged in order to effectively manage ecosystems and landscapes for multifunctionality. The underlying biological principles of ecosystem process multifunctionality have clear relevance to ecosystem service multifunctionality, and to the mapping of ecosystem services and identification of multifunctional landscapes. Land management and conservation agencies use the term 'multiple use landscapes' (Moilanen et al., 2005) to describe the tradeoffs inherent in conserving species and habitats within heterogeneous landscapes that provide a variety of ecosystem services. Joint production functions in economics are the equivalent of ecosystem multifunctionality reduced to a common denominator (money). Each of these concepts and disciplines has a great deal of conceptual and mechanistic overlap that is not currently being exploited to its full extent to develop better predictive models of ecosystem service multifunctionality and effective management strategies.

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