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CHAPTER 12

Restoring biodiversity and ecosystem function: will an integrated approach improve results?

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12.1 Introduction

Twenty years ago, Bradshaw (1987) stated that ecological restoration should be an acid test of ecological understanding. In fact, the practice of restoration has developed more through trial and error than by the application of any scientific framework. Since Bradshaw's statement, restoration ecology has undergone a rapid increase in conceptual development and basic research, as indexed by the rising number of peer-reviewed publications (Young *et al.* 2005), the creation of the journal *Restoration Ecology* in 1993, and the recent publication of a number of edited volumes dedicated to exploring the conceptual underpinning of restoration ecology (Falk *et al.* 2006, Van Andel and Aronson 2006). In addition, meta-analyses of restoration studies (e.g. Pywell *et al.* 2003) are beginning to draw out some general patterns and relate them to broader ecological theory. In this chapter we contribute to this development by exploring the applicability of the biodiversity-ecosystem functioning (BEF) framework to restoration science.

Restoration ecology is the subdiscipline of ecology that informs the 'intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability'(Ser 2004). Like the broader field of ecology, restoration ecology is an integrative discipline, having drawn important influences from fields as diverse as applied sciences such as agronomy and engineering (Mitsch 1993); social sciences such as sociology (Geist and Galatowitsch 1999) and landscape architecture (Fabos 2004); and earth sciences such as soil science (Bradshaw 1997) and hydrology (Morris 1995); as well as the subfields of population (Rosenzweig 1987) and landscape ecology (Van Diggelen 2006). This diversity of influences has led to many different approaches and goals for restoration projects. However, given the primary focus on restoring the structure and function of ecosystems, the strongest conceptual basis for most of restoration ecology stems from community and ecosystem ecology (Ehrenfeld and Toth 1997, Palmer *et al.* 1997, Young 2000, Falk *et al.* 2006). Simply put, restoration ecology is typically interested in restoring either biodiversity, ecosystem functioning, or both.

Despite these overlapping areas of interest, little crossover is evident between restoration ecology and 'classical' biodiversity-ecosystem function research (Naeem 2006a). With few exceptions (Bullock *et al.* 2001, Callaway *et al.* 2003, Bullock *et al.* 2007), BEF experiments have not taken place in restoration settings. Although BEF research might inform restoration (Aronson and Van Andel 2005, Young *et al.* 2005, Naeem 2006a), thus far few concrete suggestions have been offered on how restoration ecology might benefit from a consideration of BEF research and theory or vice versa. In this chapter, we start by comparing community and ecosystem approaches to restoration and suggest how a BEF approach might differ from these. We then draw on BEF theory and empirical research to suggest three broad areas where understanding the links between biodiversity and

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ecosystem functioning could have significant impacts on the success of restoration: 'classical' BEF impacts (i.e. higher diversity leads to improved functioning); the effects of biodiversity on the stability of ecosystem functioning; and the effects of biodiversity on the provisioning of multiple ecosystem services.

For this chapter, we constrain the scope of what we consider to be restoration to management activities whose primary goal is to improve ecosystem services other than provisioning services, although improved provisioning services may result from the activities. Management activities whose primary goal is to improve provisioning services are considered in Chapter 13, which formally examines the role of BEF research in managed ecosystems.

12.2 Community, ecosystem, and BEF approaches to restoration

BEF research combines elements from community and ecosystem ecology. Consequently, Naeem (2006a) contrasted community and ecosystem approaches to restoration with an approach based on the BEF perspective. A community approach largely focuses on the restoration of the biotic components of an ecosystem – which species are present, their relative abundance, and their interactions (trophic, competitive, facilitative). It is often used when starting from essentially bare ground, as in tallgrass prairie or hay meadow plantings in former agricultural fields, and when the goal of restoration is to enhance the conservation value of a protected landscape – restoration for biodiversity's sake. This approach has evolved over time from assuming that restoration is essentially the speeding up of a linear approach to a specific, predictable, equilibrium state, to accepting the dynamic nature of communities, possible alternative stable states (Bullock *et al.* 2002, Hobbs 2006), and the influences of disturbance and dispersal limitation on diversity (Pywell *et al.* 2003, Walker *et al.* 2004).

This evolution may help overcome some of the problems encountered when using the community approach. For example, restoring the target community is often more difficult than expected, even in systems where community restoration has been practised for decades (Kindscher and Tieszen 1998). Furthermore, restoration of one part of a community has not always yielded restoration of the whole community. In both California grasslands and English meadows, plant composition and relative abundance of species have been restored to resemble the reference condition, but the soil microbial community has remained significantly different, implying that functions such as decomposition and nutrient turnover may not have been restored (Smith *et al.* 2003, Potthoff *et al.* 2005, Steenwerth *et al.* 2006, Pywell *et al.* 2007). Although greater understanding of factors influencing community assembly may overcome some of these problems, it may not overcome the common assumption of the community approach that functioning will be restored if the community is restored. This was explicitly studied in two constructed *Spartina* marshes. In both, vegetation composition, cover, and biomass of planted sites were similar to those of natural marshes within 18 months of planting, but in one case, the height structure failed to meet the needs of the endangered bird for which the marshes were constructed (Zedler 1993), and in another, soil organic matter and nutrient accumulation, denitrification rates, and tidal export of nutrients required much longer to resemble reference levels (Craft *et al.* 1999).

The ecosystem approach makes the opposite assumption, in that a habitat template that restores ecosystem processes (e.g. hydrology of a wetland) is created, but most or all species are left to colonize on their own in a process of self-assembly (e.g. Bradshaw 2000). The approach, which is characteristic of many early restoration efforts (Bradshaw and Chadwick 1980), may more accurately be described as 'rehabilitation' rather than 'restoration' (Ser 2004). Some examples of this approach include constructing mechanical barriers in eroded gullies in an overgrazed rangeland in order to slow surface water flow and enhance water percolation into the soil (King and Hobbs 2006) and increasing meandering of a stream in order to reduce flash flooding and increase habitat complexity and sediment and nutrient retention (Rosgen 1994). Other activities using the ecosystem approach include ecological engineering and reclamation. Ecological engineering strives to achieve and maintain a specific ecosystem service within a relatively strict range, such as reducing nitrogen in wastewater to regulator-accepted standards via a constructed

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wetland. In contrast, reclamation strives to make a highly altered system serve some useful purpose by achieving an acceptable level of safety and aesthetics, such as stabilizing mine tailings with vegetation that can tolerate the harsh conditions but are not necessarily native to the site (Ser 2004). Both use ecological processes and biotic components to achieve their goals, but these goals do not include creating a system whose functioning or composition resemble a reference ecosystem.

Although economically attractive, the 'Field of Dreams' approach of solely manipulating the physical environment ('If you build it, they will come'; Hilderbrand *et al.* 2005) is risky because dispersal barriers limit the colonization of desired biotic components and, even if these can be overcome, interactions with species not yet present (e.g. pollinators or mycorrhizae) may be necessary for establishment or reproduction of important species. Furthermore, initial seeding with native or exotic species that may grow quickly and provide good cover can prevent establishment of desired later successional species. For example, in old field sites in England, sowing of a few native grasses limited successful colonization by desired species (Pywell *et al.* 2002). In addition, projects using the ecosystem approach with no attention to the composition of the biotic component may achieve their physio-chemical goals, but the narrow focus of these goals may lead to long-term problems. For example, some of today's most troublesome invasive species were introduced as a rehabilitation measure in over-grazed, drought-stressed rangelands (Christian and Wilson 1999, Clarke *et al.* 2005, Schussman *et al.* 2006, Williams and Crone 2006). Finally, the approach does not take advantage of the multiple functionality and resilience potentially provided by systems with an actively restored biotic community.

In contrast, a restoration approach based on BEF theory and empirical results stresses the relationship between the biotic community and ecosystem functioning. Although the BEF perspective does not encompass all of the topics relevant to ecological restoration, it does cover the majority of a more general framework recently proposed for restoration ecology (King and Hobbs 2006). A BEF approach to restoration is based on the asymptotic relationship between biodiversity and ecosystem functioning. This relationship is what sets the BEF approach to restoration apart from the other two approaches. Restoration strives to restore an ecosystem to that relationship by removing anthropogenic inputs that maintain high functioning but low diversity in managed systems (e.g. fertilizer or pesticides) or by enhancing functioning in degraded systems by adding key sets of species (Naeem 2006a). Debate about the applicability of BEF theory outside of experimental settings (Huston 1997,

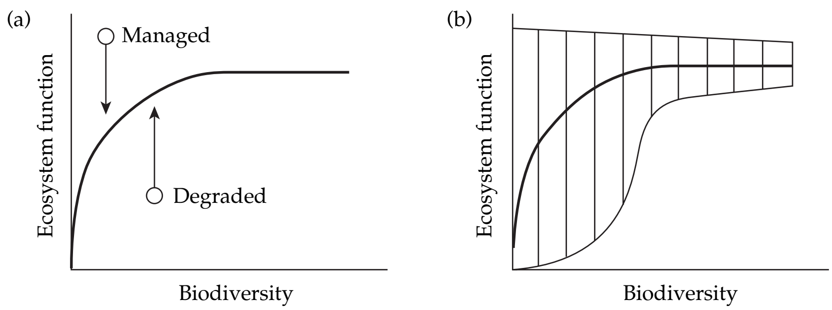

Figure 12.1 The BEF perspective for ecological restoration. (a) The fundamental assumption of the BEF perspective is that biodiversity affects ecosystem function, often in the manner depicted here, where adding diversity when diversity is low has a stronger effect on ecosystem functioning than adding diversity when diversity is high, until the point at which increasing diversity has no effect of functioning. Restoration (vertical arrows), in this perspective, is the restoration of this relationship in degraded systems, which have lower functioning than expected, or in managed systems, in which anthropogenic inputs produce functioning at a higher level than expected given the system's diversity. (b) The theoretical realm of possible ecosystem functioning in relation to biodiversity. The hatched area incorporates the assumption, supported by empirical evidence, that it is possible to have greater functioning with a low number of species than with the most diverse system, as well as the assumption that the range of variability in functioning decreases as biodiversity increases. The latter assumption has less support from empirical evidence (see text). Figure is adapted from Naeem (2006).

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Box 12.1 Should the BEF restoration approach apply to all ecosystems?

Ecological restoration, like most things ecological, is inherently and frustratingly context-dependent. Restoration is being carried out in habitats as diverse as streams, rivers, forests, wetlands, grasslands, estuaries, deserts, and alpine habitats to achieve an equally diverse suite of goals. Given the diversity of contexts in which restoration occurs, it is appropriate to ask whether the BEF approach is relevant to all forms of restoration. We see great potential for the BEF perspective to improve the practice of ecological restoration in many cases. However, it is important to recognize that in systems where abiotic structure serves as the dominant control of ecosystem properties, the BEF approach may not be as relevant to successful restoration.

Streams and rivers are an instructive case study of restoration in ecosystems that are strongly controlled by abiotic forces. River restoration is one of the most extensive forms of restoration in the USA, with at least $1 billion dollars invested annually (Bernhardt *et al.* 2005). A growing body of scientific literature has documented biodiversity effects on ecosystem function in stream ecosystems (e.g. Jonsson and Malmqvist 2000, Cardinale *et al.* 2002). Yet because the dominant taxa in river ecosystems are easily dispersed, short-lived, and small it is difficult to apply these BEF perspectives to river restoration projects. Seeding streams with the appropriate algae, macroinvertebrates, and fish is no guarantee that those organisms will establish. In terrestrial ecosystems, where vegetation itself provides much of the physical structure of the environment on which other organisms depend, it is easy to see how planting diverse native species assemblages can effectively 'restore' not only an ecosystem function (= productivity) but also key components of ecosystem structure (e.g. canopy architecture). This is not the case in rivers, where the physical template is primarily controlled by hydrology and geomorphology.

However, we would argue that a BEF perspective can and should inform river restoration in two important respects. First, terrestrial vegetation can play very important roles in river ecosystems, and thus BEF approaches can directly inform riparian management aspects of river restoration. The majority of small stream ecosystems are primarily fueled by leaf litter inputs (Fisher and Likens 1973), and higher diversity litter inputs can lead to greater secondary production (Swan and Palmer 2006). Riparian trees themselves contribute large wood to stream channels which can play important roles as both habitat and biogeochemical hotspots in rivers (Wallace *et al.* 1995, Valett *et al.* 2002, Wright and Flecker 2004, Warren and Kraft 2006).

Second, a BEF perspective should inform the evaluation of river restoration projects. Even when aquatic organisms cannot be directly introduced, monitoring changes in community composition following restoration activities can provide important insights into what is and what is not working. For example, the absence of shredding functional feeding groups from restored streams relative to reference conditions may indicate that organic matter dynamics have not been effectively restored, the presence of nitrogen-fixing blue–green algae may indicate that phosphorus loads are excessively high, or the absence of a diverse hyporheic meiofauna may suggest that groundwater and surface waters have not been effectively reconnected. While restoration practitioners may not be able to actively manage the diversity of all ecosystems to affect services, recognizing the links between biodiversity and ecosystem functioning that exist even in ecosystems strongly controlled by abiotic forces can lead to improved assessment of the success or failure of restoration projects.

Wardle 1999, Naeem 2000, Grace *et al.* 2007) has highlighted that restoring a highly diverse community does not necessarily guarantee a high level of functioning – environmental factors such as soil fertility and climate are also crucial determinants of ecosystem functioning (Huston and Mcbride 2002, Naeem 2002b). However, when environmental factors are held constant, the BEF approach suggests that greater biodiversity provides a high level of ecosystem functioning, although achieving the highest level of functioning does not require the restoration of the entire community (Lehman and Tilman 2000, Naeem 2006a). The rest of this chapter explores these implications for restoration in greater detail.

12.3 'Classical' BEF implications for restoration

Since its earliest inception BEF research has largely been focused on testing the hypothesis that the loss of diversity of species (or functional groups) leads to changes in ecosystem functions such as productivity

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Box 12.2 Diversity of grassland plantings

Grassland restoration in the central portion of the USA illustrates the relatively low level of diversity used in some restorations compared to their reference systems and the implications.

- Native northern mixed-grass prairie in western Nebraska and South Dakota has approximately 37–80 native plant species per 0.1 ha (Symstad *et al.* 2006), whereas the recommended seed mixtures for native rangeland plantings (> 0.1 ha) in this region have a maximum of 13–25 species and a minimum of four species (http://www.nrcs.usda.gov/technical/efotg/).
- The federal Conservation Reserve Program (CRP) pays farmers to plant or maintain perennial vegetative cover, grassland being one allowable type, in areas that would otherwise be used for agricultural production. The program, which affects more than 10 million ha of grassland nationwide, rewards plantings that provide ecosystem services such as reduced soil erosion, increased wildlife habitat, water quality protection, soil salinity reduction, and carbon sequestration (Barbarika 2005). The diversity of these plantings is difficult to track, but typical values are 4–10 species.
- The species planted in restorations like these are often dominants (e.g. warm-season bunchgrasses) that drive major aspects of ecosystem functioning (Camill *et al.* 2004), but low functional diversity, particularly the lack of nitrogen-fixing legumes in some plantings, may limit a restoration's functioning potential (Kindscher and Tieszen 1998).

or nutrient cycling (Naeem *et al.* 1994, Hooper and Vitousek 1997, Tilman *et al.* 1997b). Since these early studies, the field of BEF research has flourished, with over 100 published experiments testing this general hypothesis (Cardinale *et al.* 2006a). Contentious debates have ensued about the proper experimental design or how best to interpret the results of these experiments (Garnier *et al.* 1997, Huston 1997, Wardle *et al.* 1997a, Thompson *et al.* 2005, Wright *et al.* 2006), and considerable work still needs to be done to determine the mechanisms that might link diversity to ecosystem functioning. Despite these uncertainties, several recent meta-analyses have demonstrated that, on average, ecosystem functioning does increase with increasing numbers of species in BEF experiments (Balvanera *et al.* 2006, Cardinale *et al.* 2006a). For example, Cardinale and colleagues (2006a) found that diversity enhanced both plant productivity and nutrient uptake. These biodiversity effects can be tied to two ecosystem services that are often the focus of restoration efforts. It should be noted that while the most represented ecosystem in this meta-analysis were grasslands, these comprised only 34% of the studies, with the rest coming from a broad diversity of other terrestrial and aquatic ecosystems. Thus there is a growing body of work addressing BEF questions in other ecosystems such as streams (Jonsson and Malmqvist 2000, Cardinale *et al.* 2002), wetlands (Engelhardt and Ritchie 2001, Callaway *et al.* 2003, Sutton-Grier *et al.* In Review), forests (Bunker *et al.* 2005, Scherer-Lorenzen *et al.* 2005a), and marine systems (Duffy *et al.* 2001, Solan *et al.* 2004, France and Duffy 2006b, Worm *et al.* 2006). For most systems in which restoration is being conducted, potentially relevant BEF experiments have been conducted. Applying the findings from BEF research to restoration practices should be a natural extension of existing research. Indeed, a study that examined the consequences of restoring plant communities on ecosystem functioning in a California estuarine salt marsh demonstrated that increasing plant richness led to higher rates of nitrogen uptake and greater above- and below-ground biomass (Callaway *et al.* 2003). Grassland and wetland restorations typically start from bare ground and try to recreate natural communities through the addition of seed. The seed mixes used are not particularly diverse relative to the natural ecosystems that serve as restoration targets (Box 12.2). Thus, many terrestrial restoration activities are operating in the region of diversity where varying species richness is most likely to have a significant effect on ecosystem functioning, since most ecosystem functions saturate at relatively low levels of species richness (Cardinale *et al.* 2006a).

However, the application of classical BEF research to restoration activities may still be limited given our current knowledge. First, while average ecosystem function has been shown to increase with increasing diversity (Balvanera *et al.* 2006, Cardinale *et al.* 2006a), meta-analysis of BEF experiments has also demonstrated that the highest performing species in monoculture produces a level of ecosystem function that cannot be distinguished

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from the level observed in the highest diversity treatment (Cardinale *et al.* 2006a). Second, due to the constraints of experimental design, BEF experiments do not always include low-diversity polycultures capable of outperforming the highest diversity treatment (Chapter 2). Thus, if the goal of restoration is to provide a maximum level of ecosystem services, arguments could be made for establishing a high-performing species to rapidly achieve a high level of functioning early in the restoration process. However, because these high-performers are usually dominant species, subordinate species may be more difficult to establish after the fact, as observed in tallgrass prairie plantings (Weber 1999), hay meadows (Pywell *et al.* 2002) and coastal marshes (Keer and Zedler 2002). This is particularly important because there is some evidence that the effects of greater diversity on functioning take some time to develop (Tilman *et al.* 2001, Cardinale *et al.* 2007), and because these subordinate species may contribute to stability of functioning.

12.4 BEF and stability of services in restoration

The question of whether biodiversity contributes to stability (e.g. resistance to disturbance, resilience after disturbance, and moderate range of variability through time) has been a topic in ecology for more than half a century (e.g. Macarthur 1955, May 1972). The recent development of the BEF perspective has provided resolution to some aspects of this question by suggesting that species that share functional effects traits (characteristics that affect ecosystem functioning in a specific way) often differ in their functional response traits (characteristics that determine how they respond to a specific perturbation). As a result, a relatively low number of species may provide a certain level of an ecosystem function in a constant environment, but if these species are adversely affected by a perturbation (e.g. drought, flood, fire, or herbivory), that level of functioning will only be maintained if species with a similar effect on functioning respond positively to this perturbation. For example, Eviner *et al.* (2006) identified a strong seasonality in the effects of individual species on N and P cycling in northern California grasslands. Their results suggest that when in mixture, the species' contributions to ecosystem functions would vary throughout the season, providing a mechanism for maintaining these nutrient cycles throughout the season. In addition, they investigated the relationship between a variety of plant traits (live tissue and litter chemistry and biomass, modification of bioavailable C and soil microclimate) and the ecosystem functions. The influence of individual traits on N mineralization and nitrification also varied throughout the growing season, illustrating how response traits (to seasonal changes in moisture and temperature) are not necessarily correlated with functional effect traits (Landsberg 1999, Lavorel and Garnier 2001, Hooper *et al.* 2002, Naeem and Wright 2003).

Several reviews describe this and other mechanisms in greater detail and show the strong theoretical support for the diversity–stability hypothesis (McCann 2000, Cottingham *et al.* 2001, Loreau *et al.* 2002, Hooper *et al.* 2005, Chapter 6), and empirical support for the hypothesis exists from experiments in systems relevant to ecological restoration. In plots in which plant species richness varied because of nitrogen manipulations, aboveground biomass was more resistant to, and recovered more fully from, a major drought in more diverse grassland plots in central Minnesota, USA (Tilman and Downing 1994). In the same system, but in plots in which plant species richness was directly manipulated, temporal stability (measured as temporal mean/standard deviation) of aboveground plant biomass over ten years increased linearly, from approximately 3.5 to 5.8, as planted species richness increased from one to 16 species, with the diverse plots having lower temporal standard deviations for a given mean biomass than the monocultures (Tilman *et al.* 2006b). Despite these encouraging examples, there are also counter-examples. More diverse plots had lower resistance of primary productivity to drought in a Swiss grassland experiment (Pfisterer and Schmid 2002); individual species, rather than species richness, affected biomass stability in constructed or natural wetlands (Rejmankova *et al.* 1999, Engelhardt and Kadlec 2001); and rocky shore intertidal communities with the greatest diversity were most severely affected

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by heat stress (i.e. had low resistance) but the quickest to recover from the stress (i.e. high resilience) (Allison 2004). A recent meta-analysis of a large number of studies confirmed this inconsistency – averaged across experiments, more diverse systems were more resistant to nutrient perturbations or invasions, but diversity had either a neutral or negative effect on resistance to drought, response to warming, and variation in response to long-term environmental variability (Balvanera *et al.* 2006).

Maintaining ecosystem services within a reasonable range of variability is an important component of restoration projects focused on restoring functioning. The balance of evidence is currently not very strong that biodiversity plays a large role in determining this variability. However, relatively few field-scale studies have investigated this question, and there is no evidence that diversity strongly negatively affects stability, particularly over the long term, so the cost of increasing the diversity of a restoration is likely only the direct cost associated with adding that diversity.

12.5 Biodiversity and the restoration of multiple ecosystem functions

Restoration activities are not typically conducted with the goal of restoring a single ecosystem service. Rather, there is an implicit understanding that 'healthy' ecosystems provide a large number of services (Duraiappah and Naeem 2005), and that restoration can serve to increase multiple ecosystem services (Nrc 2001, Bernhardt *et al.* 2005). For example, the restoration of Iraq's Mesopotamian marshes has been assessed based on five separate ecosystem functions: productivity of the dominant plant *Phragmites australis*, redox status, hydrologic function, salinity, and bird diversity (Richardson and Hussain 2006). Similarly, the US National Resource Council suggested that five major functions of wetlands need to be considered in the construction or restoration of wetlands: hydrologic functions, water quality functions, support of vegetation, support of fauna, and soil functions (Nrc 2001).

This demand for multiple ecosystem services from a single restoration may be the strongest argument for incorporating greater biodiversity into ecological restorations. As was discussed above, high diversity plots in BEF experiments do not, on average, significantly outperform the highest performing monoculture (Cardinale *et al.* 2006a). However, what is not clear from this analysis is whether a single species can maximize the provisioning of multiple ecosystem functions. Evidence from a biodiversity, carbon dioxide, and nitrogen manipulation experiment in a Minnesota grassland context (Reich *et al.* 2001, Reich *et al.* 2004) suggests that this is not the case. In this experiment, the total above- and belowground biomass produced by a species and the amount of inorganic nitrate left in the soils after plant uptake were strongly correlated in the first year after planting (Fig. 12.2(a)). Such a result would suggest that a single species might be capable of both fixing high amounts of carbon and improving water quality by reducing nitrogen export. However, in subsequent years of the experiment, this correlation broke down (Fig. 12.2 (b,c)), making it more difficult to suggest a single species maximizes both ecosystem services. In fact, Hector and Bagchi (2007) found that maximizing seven ecosystem functions required between 8 and 16 species at eight grassland sites across Europe. In a recent review, Gamfeldt *et al.* (2008) found that multifunctional redundancy (i.e. the degree to which multiple species could sustain multiple functions) was generally lower than single-function redundancy (i.e. the degree to which multiple species could sustain a single function).

Species effects on ecosystem functions are functions of key morphological and ecophysiological traits (Engelhardt and Kadlec 2001, Eviner and Chapin 2003, Diaz *et al.* 2004), and BEF research is increasingly focused on how particular traits interact to determine the effects of diversity on ecosystem functioning (Eviner and Chapin 2003, Naeem and Wright 2003, Solan *et al.* 2004, Bunker *et al.* 2005). While attempts to determine which traits are most important in regulating particular ecosystem functions are still in the early stages, it seems reasonable to assume that different processes might be affected by different combinations of traits. Given this assumption, the extent to which single species can maximize multiple functions will depend on the extent to which the traits responsible for regulating the ecosystem functions of interest are

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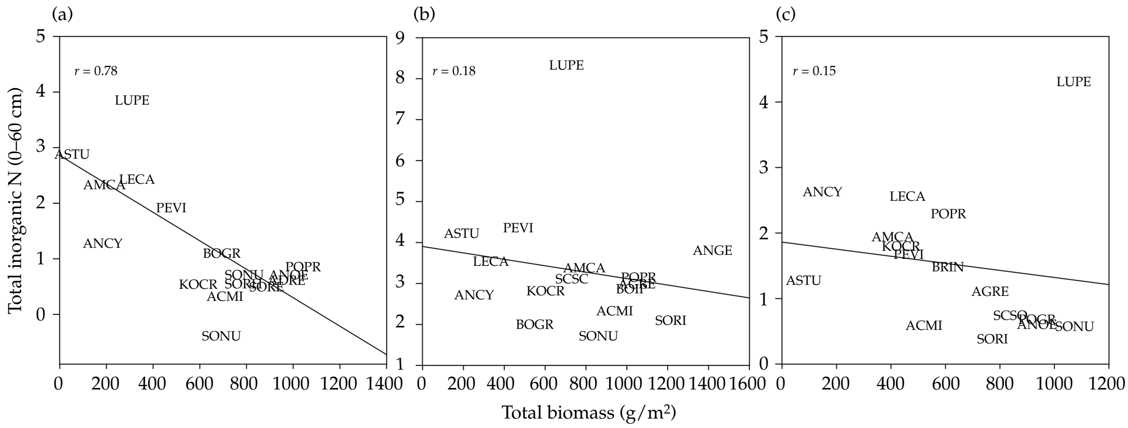

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Figure 12.2 Relationship between two ecosystem functions, total above- and belowground biomass (a surrogate for carbon storage) and total extractable soil inorganic nitrogen (a surrogate for nitrogen removal from groundwater) from monocultures of different species in control plots (ambient levels of atmospheric CO_2 and nitrogen) of the BioCON BEF experiment from (a) 1999, (b) 2000, and (c) 2001. Species codes of the monocultures are: *Achillea millefolium* ACMI; *Agropyron repens* AGRE; *Amorpha canescens* AMCA; *Andropogon gerardi* ANGE; *Anemone cylindrical* ANCY; *Asclepias tuberose* ASTU; *Bouteloua gracilis* BOGR; *Bromus inermis* BRIN; *Koeleria cristata* KOCR; *Lespedeza capitata* LECA; *Lupinus perennis* LUPE; *Petalostemum villosum* PEVI; *Poa pratensis* POPR; *Schizachyrium scoparium* SCSC; *Solidago rigida* SORI; *Sorghastrum nutans* SONU. Note that the scale changes on the axes between years.

correlated. Several recent large-scale analyses have found significant correlations between several important traits in plants (Diaz *et al.* 2004, Wright *et al.* 2004, Reich *et al.* 2006) and animals (Brown *et al.* 2004). These correlations yield suites of traits (e.g. those contributing to rapid acquisition of resources vs. those that contribute to conservation of resources in well-protected tissues in plants) that typically occur together in organisms. The uniformity of these suites across broad taxonomic groups and geographical gradients argue for the existence of fundamental tradeoffs in organismal development and life history. Whether or not these tradeoffs hold up within local species pools, where selection might push for diversification along trait axes (Grime 2006, Ackerly and Cornwell 2007), and for the traits actually responsible for ecosystem functions of interest in restoration (Eviner 2004), remains an open and important question.

12.6 The economics of BEF in restoration

For BEF research to be useful for ecological restoration, ecosystem functions must be related to the ecosystem services desired as the outcome of restoration. A key issue in performing this translation is that BEF research often does not assign a specific worth to a level of ecosystem functioning other than a vague 'more is better' for primary productivity or nutrient capture (Srivastava and Vellend 2005). In contrast, in restoration, the relative worth of various levels of ecosystem services must be assessed and agreed to by many stakeholders when any but the simplest restoration project is commenced (Fig. 12.3). Provisioning services, such as forage production, can be easily converted into currency value (Bullock *et al.* 2007). However, while Worm *et al.* (2006) showed dramatic increases in tourism-related revenue following the closure of fisheries in marine protected areas, which they attribute to increases in diversity, this conversion is not as easy for other types of ecosystem services resulting from ecological restorations. For example, results from BEF research might predict grams of carbon fixed per square metre, grams of nitrogen removed through denitrification, and grams of the greenhouse gasses N_2O and methane produced by different combinations of species used in a wetland restoration project. Until markets exist that allow translation of these ecosystem processes into a common currency, determining which mixture of species maximizes benefits while minimizing costs is, at best, just a guess. The growth of carbon trading markets (Bonnie *et al.* 2002) and early

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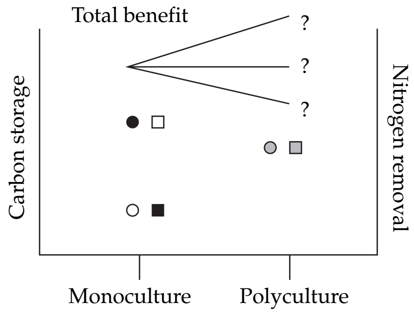

Figure 12.3 Hypothetical restoration scenario involving two ecosystem services: carbon storage (circles) and nitrogen removal (squares). Managers could choose between planting a monoculture of species 1 (filled symbols) that provides high levels of carbon storage but low levels of nitrogen removal, a monoculture of species 2 (open symbols) that provides low levels of carbon storage but high levels of nitrogen removal, or a mixture of both species that provides intermediate levels of both carbon storage and nitrogen removal. The total benefit of the ecosystem services provided by these different management choices (straight lines) is unknown and will depend both on the shape of the relationship between diversity and these two functions and on the relative economic weight placed on the two services.

attempts at nitrogen trading schemes such as the EPA's Water Quality Trading Program (active in areas of 10 states in the USA) suggests that economic valuations of at least some of the non-provisioning ecosystem services provided by restored ecosystems are being developed. An even more difficult task is deriving a common currency for services such as protecting higher trophic levels or maintaining hydrologic services, although tools for evaluating different options in the face of such uncertainties do exist (Lynam *et al.* 2007).

12.7 Recommendations

We argue that understanding the relationship between biodiversity and ecosystem functioning is important in enhancing restoration success in many ecosystems and that restoration activities can serve as powerful tools for exploring some of the central BEF questions. However, information exchange between the scientific community and restoration practitioners is too little and too slow for BEF research to be relevant in adaptive management of degraded ecosystems. Ecologists are recognizing that performing policy-relevant science involves more than simply publishing in high-profile academic journals (Palmer *et al.* 2004). This point is reinforced by a recent survey of stream restoration practitioners that showed that less than 1 per cent of over 300 restoration projects had specifically been informed by results published in scientific journals (Bernhardt *et al.* 2007). So what can be done to improve the situation?

For scientists, we make a few suggestions. First, continue basic BEF research, but keep in mind the information needed by restoration practitioners. Deeper understanding of how functional traits acting alone and in combination affect ecosystem functions that are related to ecosystem services is particularly important. Although general relationships between diversity and functioning explain why the restoration of biodiversity is important for restoring ecosystem functioning, restoration practitioners ultimately need to know which specific species combinations to restore and have confidence in the outcome of restoration projects. However, BEF theory, while explanatory, is not yet predictive (Hooper *et al.* 2005) and is therefore not yet ready to be embraced by the management community. Furthermore, experimental perturbations in BEF experiments, and monitoring of experiments over long time periods in which the environment fluctuates naturally, will help resolve what role biodiversity plays in stabilizing ecosystem services. However, because species and communities respond to environmental fluctuations in seemingly idiosyncratic ways, investigations that tie these two themes together, by seeking patterns in traits that determine species' responses to environmental variations, will yield the most relevant information for restoration.

BEF research focusing on microbial diversity is particularly crucial because many of the most critical ecosystem services are underpinned by microbial processes (e.g. the nutrient transformations that improve water quality). Our understanding of both how plant and animal diversity affect microbial community structure and how microbial diversity directly affects ecosystem functioning in real systems is relatively weak (Fierer *et al.* 2007, Jackson *et al.* 2007). To date there has been little focus on the importance of restoring microbial communities or how to go about doing so (Hasselwandter 1997). Restoration of the

From: Biodiversity, ecosystem functioning and human wellbeing. (2009). Oxford University Press
eds S. Naeem, D. E. Bunker, A. Hector, M. Loreau & C. Perrings, pp. 167-177

microbial community in meadows were not achieved by a simple soil microbe addition technique (Pywell *et al.* 2007), but experiments have shown that microbial community composition is related to both the diversity of the restored plant communities and to particular 'facilitating' plant species (Smith *et al.* 2003, Bardgett *et al.* 2006). A deeper understanding of the controls and consequences of microbial diversity is an area where BEF research is well-poised to make important contributions to restoration ecology.

Another aspect of diversity that may be critical to restoration success, but has been not been as extensively studied in BEF research, is the importance of genetic diversity. Many ecosystems, including many that are important targets for restoration, are dominated by a single species that controls ecosystem function, e.g. giant kelp in kelp forests, Ponderosa pine in many forests of the Western US, seagrasses such as *Zostera marina* in shallow estuarine systems, and *Spartina* in intertidal zones. A growing body of work is showing that genetic diversity within a species can be an important regulator of ecosystem function (Hughes *et al.* 2008). Work on *Zostera*, an important species in estuarine restoration, showed that clonal diversity measurably affects ecosystem processes or the stability of those processes (Hughes and Stachowicz 2004, Reusch *et al.* 2005). Williams (2001) demonstrated that reduced genetic variation in *Zostera* used in restoration efforts resulted in decreased population growth and individual fitness. For both cottonwood (*Populus fremontii* x *augustifolia*) (Schweitzer *et al.* 2005a) and apsen (*Populus tremuloides*) (Madritch *et al.* 2006), genotypic richness can affect decomposition rates and nutrient cycling. Clonal diversity of *Solidago altissima* were shown to affect, not only primary productivity, but the diversity of higher trophic levels (Crutsinger *et al.* 2006). Given these compelling examples, research on the consequences of genetic diversity of species commonly used in restoration is likely to yield benefits both to basic science and restoration.

Third, to make the results of any BEF research applicable to practitioners, the connection from biodiversity to function to services needs to be stronger. For example, although the positive effects of plant diversity on above- and belowground biomass production in grassland experiments have been vaguely related to forage production, carbon storage, and soil erosion, little attention has been paid to whether the nutrient content of the biomass is sufficient for the purported foragers (see Bullock *et al.* 2007 for an exception) and direct measurements of soil movement or long-term C sequestration are rare (though more common in wetland studies). Given the need of many restorations to restore multiple services, this connection needs to be made simultaneously for multiple functions and their related services. Addressing these issues is already one of the central thrusts of the next generation of BEF research (Naeem and Wright 2003) and should not require significant changes to how we proceed with our science beyond the functions and properties measured in typical BEF experiments.

Fourth, evaluate the relevance of experiments to real-world conditions. There is some conflict between the typical BEF experiment, which is carefully designed to disentangle the effects of individual species, functional traits, and diversity *per se* on the functions measured, and restoration projects, which are concerned with achieving a desired result with available materials and limited financial resources. Restoration practitioners may look at the high density of expensive species (many forbs, for example) planted in some BEF experiments and question the applicability of the results to their work: does the diversity effect require this relatively high input of normally subordinate or rare species? They might also question the relatively controlled situations of the field experiments: would the results be the same if vertebrate herbivores were not excluded from the plots, or if colonizing species were not removed? Finally, a practitioner would never think of restoring a *Spartina alterniflora* marsh without *Spartina alterniflora*, but many BEF studies include treatments analogous to this situation. Of greater interest to a restoration practitioner would be the question of how strong the diversity effect is when the only portion of diversity manipulated is the subordinate and rare species. These subordinate species may be essential to certain key functions which define the success or failure of the restoration. For example, grassland restoration in the UK to meet national Biodiversity Action Plan targets requires the presence of food plants of certain declining butterflies and other

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insects, but these plants are often uncommon and particularly difficult to establish (Pywell *et al.* 2003). Thus, BEF researchers seeking to provide answers for restoration practitioners and other natural resource managers need to ensure that they design their experiments with these issues in mind.

Concurrently, restoration practitioners and ecologists can potentially contribute significantly to strengthen BEF research. For them, we stress the utmost importance of monitoring and reporting short- and long-term effects of various restoration projects and practices. In the US, the federal government pays private land owners millions of dollars each year to plant and maintain perennial grasslands through the Conservation Reserve Program. A landowner's proposal is more likely to be funded if s/he plants a higher diversity of species (Usda 2006), but follow-up on the establishment success and environmental benefits of individual plantings is rare, and only recently have comparisons among the ecosystem services provided by plantings of different diversity levels been explored. In the USA, a major source of funding for stream and wetland restoration is associated with mitigation of wetland losses under the Clean Water Act (Nrc 2001). Guidelines for successful restoration vary from state to state, but typically involve recommended species lists and some assessment of total vegetation cover. Some states are currently developing improved vegetation assessments that include repeated measurements of the cover of all planted and unplanted species. In the case of North Carolina, this improved monitoring scheme has been developed in coordination with the Carolina Vegetation Survey to ensure that monitoring data can be directly incorporated into an existing vegetation database that is actively being used in ecological research (Lee *et al.* 2007). As a member of the European Union, the UK Government pays out many millions of pounds a year in funding restoration on farmland under the Environmental Stewardship scheme (http://www.defra.gov.uk/erdp/schemes/es/). This scheme exemplifies the biodiversity or ecosystem service dichotomy. Certain activities aim to restore a service, such as sowing field margins with a mix of plants designed to provide pollen and nectar for bees and butterflies or to provide winter seed for birds. In these cases the plant mixture does not resemble any seen in (semi-) natural systems and often contains non-natives. Other activities are focused on biodiversity, such as the sowing of specific plant mixtures into bare arable land or species-poor grasslands to restore particular target species-rich grasslands. Certain authors have criticized the effectiveness of European agri-environment schemes (e.g. Kleijn *et al.* 2006). This is partly because these authors have confused the aims of different activities (e.g. expecting the bird-seed mixtures to restore rare arable weed communities), but also because monitoring of outcomes has been poor. The limited monitoring (e.g. Critchley *et al.* 2004, Feehan *et al.* 2005) of vegetation has shown some success, but suggests that better targeting and more precise methods are required. This is leading to planning for more extensive and repeated monitoring programs and consideration of how biodiversity and ecosystem service aims might be integrated (e.g. for soil conservation).

Clearly, BEF research still has many avenues to explore before the majority of questions surrounding the relationship between biodiversity and ecosystem functioning are answered. Just as clearly, restoration ecology still has a long way to go before the results of reconstructing an ecosystem can be as predictable as the construction of a bridge or even a space station. Although not all restoration projects are suited to answering basic science questions regarding the relationship between biodiversity and ecosystem functioning, they are crucial to making BEF science applicable to real-world situations. Direct partnerships between researchers testing BEF concepts and restoration practitioners are crucial for ecological restoration live up to its potential as an acid test for BEF ecology.