Transferring biodiversity-ecosystem function research to the management of 'real-world' ecosystems

Running title: Transferring BEF research

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Abstract

Biodiversity-ecosystem functioning (BEF) research grew rapidly following concerns that biodiversity loss would negatively affect ecosystem functions and the ecosystem services they underpin. However, despite evidence that biodiversity strongly affects ecosystem function, the influence of BEF research upon policy and the management of 'real-world' ecosystems, i.e. semi-natural habitats and agroecosystems, has been limited. Here, we address this issue by classifying BEF research into three clusters based on the degree of human control over species composition and the spatial scale, in terms of grain, of the investigation, and discussing how the research of each cluster is best suited to inform particular fields of ecosystem management. Research in the first cluster, small-grain highly controlled studies, is best able to provide general insights into mechanisms and to inform the management of species-poor and highly managed systems such as croplands, plantations, and the restoration of heavily degraded ecosystems. Research from the second cluster, small-grain observational studies, and species removal and addition studies, may allow for direct predictions of the impacts of species loss in specific semi-natural ecosystems. Research in the third cluster, large-grain uncontrolled studies, may best inform landscape scale management and national-scale policy. We discuss barriers to transfer within each cluster and suggest how new research and knowledge exchange mechanisms may overcome these challenges. To meet the potential for BEF research to address global challenges, we recommend transdisciplinary research that goes beyond these current clusters and considers the social-ecological context of the ecosystems in which BEF knowledge is generated. This requires recognizing the social and economic value of biodiversity for ecosystem services at scales, and in units, that matter to land managers and policy makers.

Key words

BEF research; Biodiversity experiments, Ecosystem services; Grasslands; Ecosystem management, Knowledge transfer

Introduction

Widespread concerns over the consequences of global biodiversity loss led to an explosion of ecological research in the early 1990s into the relationship between biodiversity and the functioning of ecosystems (hereafter BEF research) (Schulze and Mooney, 1994; Loreau et al., 2001; Hooper et al., 2005, Eisenhauer et al., 2019 this issue; Hines et al. 2019 this issue). Historically, most work in this field has been conducted in experimental settings, especially in grasslands, where extinction is simulated by randomly assembling plant communities differing in species and functional richness and where other environmental drivers of ecosystem function are controlled for (Hector et al., 1999; Tilman et al, 2001; Weisser et al, 2017). While this work has led to several robust conclusions regarding the form of biodiversity-function relationships and the mechanisms that drive them (Cardinale et al, 2012), there remain doubts regarding the capacity for experimental BEF research to inform the management of biodiversity and ecosystem functions and services in the 'real world' (i.e. ecosystems with communities that have not been experimentally manipulated) (Huston 1997; Lepš 2004; Srivistava & Vellend 2005; Wardle, 2016; Eisenhauer ~~et al~~., 2016). Much of this debate concerns the design of biodiversity experiments, which were established to investigate if biodiversity *could* affect function, and via what mechanisms (Tilman et al., 1996; Loreau and Hector, 2001, Schmid et al. 2002).

A more recent generation of BEF research has been conducted in non-experimental and naturally assembled real-world ecosystems such as natural and semi-natural (hereafter semi-natural) drylands, grasslands and forests (e.g., Maestre et al., 2012; Grace et al., 2016; Van Der Plas et al.; 2016, Duffy et al., 2017; Fanin et al., 2018; Hautier et al.; 2018, van der Plas 2019). As they are performed in naturally assembled communities, shaped by both environmental drivers and global change factors, these studies are correlational and tend to rely upon statistical controls, thus limiting confident inference about the functional consequences of biodiversity loss in these systems. Removal experiments can help overcome this issue but, to date, relatively few have been conducted (Díaz et al 2003; Fry et al. 2013; Fanin et al. 2018). While a lack of confident inference may limit transfer, many other knowledge gaps also limit the transferability of BEF research. For example, there is little consensus regarding how important biodiversity loss is relative to other drivers of ecosystem functioning (Strivistava & Vellend 2005; Hooper et al 2012; Duffy et al 2017, van der Plas 2019). Moreover, the functional consequences of the non-random extinction which occurs in semi-natural ecosystems have largely been estimated from correlational studies (Larsen et al. 2005, Duffy et al 2017; van der Plas et al 2019a, but see Lyons & Schwarz 2001 and Zavaleta and Hulvey 2004). Further challenges in the knowledge transfer and application of BEF research emerge from a lack of information regarding the social and economic barriers to conserving biodiversity and promoting diversification (Fazey et al 2013, Rosa et al. 2019). Filling these knowledge gaps would help in providing reliable evidence to inform the management of the world´s ecosystems, e.g. via the Intergovernmental Science-Policy Panel on Biodiversity and Ecosystem Services (IPBES) (Díaz et al., 2015; Díaz et al., 2018).

In this article, we review the current understanding of the BEF relationship and discuss how BEF research could inform the management of real-world ecosystems. We do this by assessing the suitability of current knowledge for transfer and how this is reflected in current applied research. We then identify barriers to transfer and expand on how these barriers can be overcome via future research and changes to knowledge exchange mechanisms. Throughout, we emphasize the transition of BEF research from a fundamental science to applied research that can inform management. By doing so we assume that the promotion of certain ecosystem services is desired (e.g. carbon storage or crop production).

To aid understanding of the potential transfer of BEF research, we classify it into three clusters based upon a) the degree of human control over the plant community, which in experiments manifests through removal of non-target species, and in real world ecosystems through management inputs, and b) the size of the study plots or area, i.e. grain (Fig. 1a). While these two axes represent continuous gradients, and some studies are difficult to classify, research within each cluster shares several features (described below), making a general critique possible. Furthermore, each of these clusters shares features with a subset of real-world ecosystems (e.g. similar levels of human control over plant community and the grain of management (Fig. 1b). Based on these similarities, we suggest possibilities and challenges for knowledge transfer and applications. We then identify future research needs (summarized in Table 1). Throughout our discussion, we focus on terrestrial ecosystems, particularly the role of plant diversity in grasslands and that of insects in agricultural landscapes. This is because of our own expertise and the historical focus of much BEF research on these systems (Hines et al. 2019 this issue).

>Figure 1 here

Small-grain and highly-controlled experiments (Cluster A)

Since the mid 90's, more than 600 experiments have been established to explore the causal relationship between biodiversity and ecosystem functioning (Cardinale et al. 2012), typically under field conditions (e.g. Tilman 1996; Hector et al., 1999; Roscher et al., 2004). The primary goal of these experiments was to establish whether biodiversity could affect ecosystem functioning, and so they controlled for potentially confounding effects of environmental conditions, functional composition, individual density, and non-random assembly and disassembly processes (Schmid et al. 2002, Schmid and Hector 2004, Eisenhauer et al. 2019, this issue). To achieve this, BEF experiments apply a diversity treatment where varying levels of plants species richness are sown or planted, and ecosystem functioning is measured (Schmid et al. 2002, Bruehlheide et al. 2014). As such studies are highly controlled (e.g. via randomized blocking, weeding and the homogenization of growing conditions), diversity effects may be ascribed with confidence and detailed inferences can be made regarding the identity of the mechanisms driving biodiversity effects (Loreau and Hector 2001).

While these experiments act as model systems for BEF research, with generally applicable results to a wide range of systems (Schmid & Hector 2004, Eisenhauer et al., 2016), the direct application of these insights in the management of real-world ecosystems could be limited for several reasons. First, the sown or planted community (and its species richness) is maintained through the repeated removal of non-target species, which typically does not occur in real-world systems. As a result communities which would not persist without human intervention may be present. Second, the species richness gradient tends to span levels of diversity (typically 1- <20 plant species) that are much lower than many semi-natural communities (Wilson et al. 2012). Third, the studies tend to be conducted in replicated plots smaller than 500 m^2 (Tilman 1996; Hector et al., 1999; Roscher et al., 2004), with a median size of 3 m^2 (Cardinale et al 2012). As such studies are labor-intensive, they also tend to be unreplicated at the landscape scale (but see Hector et al 1999, Kirwan et al. 2007). However, the large number of experiments with comparable designs allows ~~meta-level analyses~~ to be conducted (Balvanera et al 2006, Isbell et al., 2015; Lefcheck et al., 2015, Verheyen et al 2016, Craven et al. 2018).

What can be transferred

BEF experiments were designed to provide general mechanistic insights into the BEF relationship. Nevertheless, the close control of plant community composition and their low species diversity means that findings from BEF experiments are potentially transferable to highly managed ecosystems, e.g. intensive agricultural grasslands, plantation forestry, gardens, sown communities found in urban green spaces or ecosystems restored from a heavily degraded state (Fig. 1b). Such systems tend to be managed intensively and at small scales, e.g. via the application of selective herbicides, weeding and fertilization. As these systems typically contain fewer species than most semi-natural ecosystems, we predict that BEF research is best able to inform work related to diversification, rather than the impacts of species loss. BEF experiment results suggest that diversification of such systems would lead to considerable gains in the supply of some ecosystem services, as numerous functions related to agricultural production and sustainability often increase with species diversity, including plant productivity, pollination, soil carbon storage and weed suppression (Isbell et al., 2017). Moreover, species-rich communities produce a more stable and constant yield (Isbell et al. 2015, Craven et al. 2018), which may reduce risks to farmers (Finger & Buchmann 2015).

Experimental results indicate that the benefits of diversification are greater when increasing diversity from low to intermediate levels (e.g. from 1 to 8 grassland species per m^2) than from medium to high (e.g. from 8 to 16), as the diversity-function relationship tends to saturate (Isbell et al. 2017). As species are typically grown in monocultures and in a wide range of low-diversity mixtures, data from these experiments can help to identify high performing species, but also high performing mixtures, for a range of ecosystem functions. Agronomists have conducted significant research on crop diversification for many years (Vandermeer 1992, Brooker et al. 2015), and demonstrated that crop diversification can lead to various positive outcomes, such as increased primary crop yield and biocontrol (Iverson et al 2014). Moreover, intercropping can improve yield stability (Raseduzzaman & Jensen 2017), and more diverse mixtures of cover crops, especially those containing legumes, lead to multiple additional benefits (Storkey et al., 2015; Blesh, 2018), thus increasing their multifunctionality (defined here as ecosystem service multifunctionality, the co-supply of multiple ecosystem services relative to their human demand, Manning et al 2018). Similarly, crop mixtures of multiple cultivars provide higher yields (Reiss and Drinkwater, 2018), and the mixing of rice varieties within a field reduces disease prevalence (Zhu et al., 2000). The frameworks and fundamental insights of BEF research may inform such research by identifying general rules governing complementary combinations of species and varieties (Brooker et al. 2015, Wright et al. 2017).

An additional benefit of BEF experiments is that they often provide information a wider range of ecosystem services than many agricultural experiments and agronomic analyses, which tend to focus on yield and its sustainability, e.g. weed control and nutrient cycling (Meyer et al. 2018). Mixtures that promote the supply of multiple ecosystem services simultaneously may therefore be identified from BEF studies (Storkey et al 2015, Baeten et al 2019). Further evidence of existing BEF transfer comes from grassland studies, which indicate that there are multiple benefits of diversifying agroecosystems in terms of grass yield and reduced weed abundance (Finn et al., 2013). Studies that assess the bioenergy potential of more diverse grassland mixtures have found positive diversity effects (Khalsa et al. 2004, Tilman et al 2006). However, a study of bioenergy production in grass mixtures showed that diverse mixtures were not more productive than currently used monocultures, thus showing that diversification might not always promote bioenergy production (Dickson and Gross, 2015). Even in the absence of positive impacts of diversity on productivity, other benefits may be realized; diverse bioenergy landscapes can promote the supply of other ecosystem services including greenhouse gas mitigation, pest suppression, pollination, and bird watching potential (Werling et al 2014).

A number of other avenues of experimental BEF research have the capacity to inform the management of intensive systems. BEF experiments show that damage to plant growth and productivity from plant pathogens and pests is often weaker in more diverse communities, both aboveground (Otway et al., 2005; Civitello et al., 2015) and belowground (Maron et al., 2011; Schnitzer et al., 2011). Accordingly, information from BEF experiments on plant-soil feedbacks (e.g. Vogel et al. 2019a this issue) could potentially help to devise effective crop rotation sequences , e.g. by identifying consistent antagonistic or synergistic feedbacks between functional groups when grown together or in sequence (Barel et al. 2018; Ingerslew 2018). The insights of BEF experiments are also applicable to the gardens and green roof planting (Lundholm et al 2010) and the restoration of highly degraded ecosystems. Here it may be possible to determine species mixtures or particular functional trait combinations, which, when sown or planted, deliver desired functions, such as soil aggregate stability and soil organic matter accumulation (Lange et al 2015; Gould et al 2016; Kollmann et al. 2016 Yang et al 2019). In restoration, another promising approach would be to identify and sow mixtures of species that facilitate each other as this is a key mechanism underlying biodiversity effects in harsh environments (Wright et al., 2017). Finally, evidence from forests suggests that similar or higher amounts of timber production can be achieved in mixed plantations of native species compared to monocultures of plantation species, and that co-benefits, e.g. to biodiversity conservation, would also be realized (Pretzsch & Schütze 2009, Hulvey et al 2013, Gamfeldt et al 2013, Huang et al 2018). As with crops, the results of BEF studies can also be used to indicate the tree species mixtures that best achieve this multifunctionality (Teuscher et al 2016, Baeten et al 2019).

Barriers to transfer and directions for future research

While the plant communities of BEF experiments and human-dominated ecosystems share similarities, there are also marked differences. For instance, the species composition in BEF experiments is randomly assembled and they are usually performed in unfertilized, pesticide-free, unirrigated systems. In contrast, in intensively managed real-world systems, prior knowledge has led managers to select high performing, but often low diversity, mixtures by sowing and planting species which deliver high levels of desired services, and/or encouraging these via pesticide application, irrigation and fertilization. The benefits of diversification therefore need to be demonstrated relative to these intensive low diversity communities, rather than the random low diversity assemblages found in BEF experiments. For example, in European grasslands farmers typically sow or maintain mixtures of a single grass, *Lolium perenne,* and a single legume, *Trifolium repens,* to which fertilizers are also applied (Peeters et al 2014). Such a mixture clearly differs from the random species-poor mixtures of grassland biodiversity experiments. It is unclear if the relatively diverse and high-functioning communities of biodiversity experiments are generally able to deliver yield of a similar or higher quality, quantity and reliability. However, it has been demonstrated that diversification from 1-2 to 3-4 species provides significant increases in grassland yield and higher resistance to weed invasion (Kirwan et al 2007; Nyfeler et al 2009, Finn et al 2013). We hypothesize that the species-poor communities found in intensively managed systems are more likely to resemble the high performing species-poor communities of BEF experiments (e.g. those dominated tall grasses of fertile conditions) than the low performing communities, which may struggle to persist without regular weeding and close control (e.g. those containing only a few small herbs). In contrast, the low diversity situations found in experiments, where potentially dominant species are missing, could be relevant to isolated habitat patches, where species cannot disperse to potentially suitable conditions and the species pool is restricted.

As described above, current research suggests that links between BEF and agronomic research are beginning to emerge. However, current studies do not cover the wide range of situations in which diversification could be beneficial to agroecosystems. To the best of our knowledge, little work has yet made the transition to widespread adoption, an exception being the standard mixtures for forage production in Switzerland (see Fig. 2 for details). This lack of adoption highlights knowledge exchange as an important bottleneck and another future need. To enable this, future BEF experiments could increase their relevance for management by drawing experimental communities from species pools that contain potentially useful and manageable species, and performing experiments in settings that are similar to those found in land use systems (e.g. fertilized or grazed grasslands). In this way, communities that are manageable and multifunctional may also be identified, and specific mixtures can be recommended (e.g. current policy in Switzerland). These should be cost-efficient and self-supporting and thus easily adapted and maintained by land managers.

Results on the relationship between biodiversity and the stability of ecosystem functions and services also require re-interpretation if they are to inform ecosystem management. While definitions of stability very greatly (Wissel & Grimm 1997), BEF studies typically measure stability as the coefficient of variation (e.g. Craven et al. 2018, Knapp and van der Heijden 2018), the resistance to perturbations, or the rate of recovery following these (Isbell et al. 2015). In contrast, ecosystem managers often perceive stability differently (Dongahue et al., 2016); while reliability is appreciated there are minimum levels of ecosystem service supply that are acceptable and over-performance (e.g. high productivity in favorable weather years, Wright et al. 2015) is often appreciated. Therefore, alternative measures of stability, e.g. that measure the number of years in which the supply of services exceed an acceptable threshold (Oliver et al., 2015), need to be employed if diversity-stability relationships are to be determined meaningfully for agroecosystems.

Finally, the transfer of BEF research findings to the real world may be limited by the uncertainties related to the profitability and management associated with diversifying species-poor communities and maintaining high species richness. For example, in many agricultural grasslands, plant species loss and dominance by a few nitrophilous species has occurred due to fertilization (Gaujour et al 2012, Gossner et al., 2016). Reducing nutrient availability after and reversing these biodiversity declines can be difficult (Smith et al., 2008; Clark and Tilman, 2010; Storkey et al., 2015). Moreover, species-rich seed mixtures may prove expensive to create, and it remains to be seen if diverse and high functioning grasslands can be created and maintained cost-effectively over large areas. In croplands, multispecies mixtures might pose challenges to harvesting and sorting, as most modern agricultural machinery specializes in managing and cropping monocultures and the harvesting of mixtures is relatively costly and labor-intensive (Magrini et al., 2011). We therefore need to know if, and under which conditions, encouraging diversity in agricultural systems is efficient and feasible, especially compared to management practices that deliver similar benefits (e.g. the promotion of productivity via diversification versus fertilization) (Kleijn et al. 2019). A key part of this may be to acknowledge additional benefits of diversity (e.g. pest control, pollination or higher yield stability) and to factor this multifunctionality into comparisons. To better inform the management of agroecosystems and potentially lead to their diversification, a new generation of more applied and social-ecological BEF research is required (Geertsema et al., 2016). In this new work, comparisons should be made between the 'high performing low-diversity systems' that are the current norm and multifunctional 'sustainable high-diversity systems' that can be established and maintained at an equivalent cost to current systems, or which provide additional benefits that justify greater cost (e.g. carbon storage or avoided emissions) (Binder et al., 2018). Alternatively, evidence that high diversity systems can be sustainably intensified is required, e.g. as demonstrated for biofuel grasslands (Yang et al 2018). Clearly, such approaches require transdisciplinary research involving economic and/or multiple stakeholder-based assessments of the value of the diverse systems relative to current and future systems and practices (Jackson et al 2012, Geertsema et al., 2016; Bretagnolle et al 2018, Kleijn et al 2019) (Table 1).

Cluster B) Small-grain studies with low experimental control

The second cluster contains small-grain observational studies that investigate natural- or human-induced gradients of plant diversity in less intensively managed systems (e.g. Kahmen et al. 2005a; Maestre et al., 2012; Soliveres et al., 2016a; van der Plas et al., 2016, Zhu et al., 2016) (Fig. 1). In this cluster, we also consider experiments in which particular species or functional groups are removed from intact ecosystems, often according to simulated global change scenarios (Smith & Knapp 2003; Cross & Harte, 2007; Suding et al., 2008, Fry et al. 2013, Pan et al. 2016, Fanin et al. 2018), and those which boost diversity in established communities or disturbed sites, e.g. via seeding (van der Putten et al. 2000, Bullock et al 2007, Stein et al. 2008, Weidlich et al. 2017). Finally, we also consider global change driver experiments, where biodiversity change is treated as a co-variate and used to explain observed changes in function (e.g. Grace et al., 2016; Hautier et al., 2018). Plot sizes are similar to those in cluster A (i.e. $<500m^2$) and diversity levels vary greatly, from inherently species-poor ecosystems (e.g. Suding et al., 2008) to species-rich communities (Allan et al., 2015). Therefore, in contrast to most of the experiments of cluster A, studies from cluster B tend to contain more mature communities with higher species richness, fewer monocultures, less or no weeding, and species compositions and management regimes that are more similar to real-world low management intensity systems. In most of these studies, and in contrast to most BEF experiments that manipulate random community assembly, diversity loss occurs as non-random disassembly in response to environmental drivers. Observational studies of cluster B often statistically control for co-varying factors that may also drive ecosystem functions. These may include biotic covariates, such as functional composition and the abundance of different functional groups (Maestre et al., 2012; Allan et al., 2015; Soliveres et al., 2016a; Soliveres et al., 2016b; Van Der Plas et al., 2016), which strongly co-vary with diversity in many communities (Allan et al., 2015; Barnes et al. 2016, Soliveres et al., 2016).

The design of studies in this cluster limits interpretation about the cause of biodiversity effects as data for monoculture performances are usually unavailable, meaning that the mechanisms underlying biodiversity effects cannot be estimated (Loreau & Hector 2001). This is unfortunate as these processes may differ in their strength compared to biodiversity experiments. For example, in mature communities, species may show higher levels of niche differentiation at both between and within species levels (Zuppinger-Dingley et al., 2014, Guimarães-Steinicke et al. 2019, this issue). A final property differentiating cluster B studies from those of cluster A is that variation in the diversity of other trophic levels is a complex product of responses to environmental drivers and concurrent changes in all trophic levels (Tscharntke et al., 2005, Soliveres et al. 2016a,b), rather than primarily driven by variation in the diversity of primary producers (Scherber et al. 2010).

What can be transferred

Because they are conducted in unmanipulated real-world ecosystems, cluster B results are transferable to semi-natural ecosystems, which experience species loss and compositional change due to global environmental change. Cluster B studies provide direct estimates of the real-world impacts of global change drivers on diversity, and the corresponding impact of these changes on ecosystem function. However, most cluster B studies are observational, so patterns remain correlational, despite statistical controls. Nevertheless, due to their greater realism, syntheses of cluster B results (van der Plas 2019a), can provide statistical estimates of where different components of biodiversity play their greatest role, and estimates may be used as an evidence base for both local managers and in global assessments.

The experimental studies of cluster B can provide information on how diversification can boost ecosystem functioning in restored or enriched communities. For example, several studies show that sowing into intact communities can increase both species richness and ecosystem functioning, including community productivity and carbon storage (Bullock et al 2007, Stein et al. 2008, Weidlich et al. 2018).

Barriers to transfer and directions for future research

For research in cluster B to become more directly transferable to the management of semi-natural ecosystems, greater confidence in the mechanisms underlying real-world BEF relationships is needed. While management recommendations may be drawn from selected case studies such as those presented above, a general understanding of the relative and interacting roles of environmental covariates, direct effects of global change drivers and various facets of diversity and compositional change is lacking (van der Plas 2019a). Biodiversity could play an important role in maintaining ecosystem function in real world ecosystems. Yet, whether loss of a few species at this scale makes a strong contribution to function, relative to these other drivers, has ~~been~~ only been tested in a limited number of cases (e.g. Manning et al. 2006; Allan et al. 2015; Winfree et al. 2015; Grace et al., 2016), and inconsistently, making generalization difficult (van der Plas 2019a). To address this issue, observational studies need to ensure that factors such as abundance and functional composition are properly controlled for statistically. By combining estimates of expected biodiversity change according to different global change drivers across a range of conditions (e.g. Grace et al., 2016; Hautier et al., 2018, Bjorkman et al 2018), knowledge of how great a difference to functions and services such changes will make (e.g. Craven et al 2018), and ecosystem service production functions, predictions of the impacts of drivers on ecosystem services can be made (Isbell et al 2015). This in turn allows for estimates of where ecosystem service-based arguments for conservation are strongest. Such predictions, if verified, could then form a sound basis for management decisions.

Transfer would also be enabled by a new generation of experiments. These could include a wider range of non-random extinction scenarios, assessments of the relative importance of abiotic drivers of function and biodiversity (e.g. Manning et al., 2006; Isbell et al., 2013), and the reduction of diversity from high to intermediate levels (Zobel et al. 1994), in order to verify, or refute the results of observational studies. To do this, manipulations such as the manipulation of dominance and functional composition, trait dissimilarity, or other aspects of biodiversity could be employed (Smith and Knapp, 2003; Manning et al., 2006; Cross and Harte, 2007). Manipulations that simulate the homogenization of biota (i.e. the loss of beta diversity, while alpha diversity remains unchanged), may also prove informative, as this may be as, or more, common than alpha diversity loss in real-world ecosystems

(Flohre et al., 2011; Vellend et al., 2014; Dornelas et al., 2014; Gossner et al., 2016; Wardle 2016). Finally, it may be possible to link community assembly mechanisms (e.g. founder effects and habitat filtering) and functional BEF research to identify how to increase species richness and promote certain ecosystem functions, information that would be particularly useful in ecosystem restoration (Bullock et al 2007, Stein et al. 2008, Kirmer et al 2012, Weidlich et al. 2018) (Table 1).

Work is also needed in converting the measures of ecosystem function commonly taken in ecological studies into measures of ecosystem services that are of relevance to stakeholders (Mace et al 2012, Kleijn et al. 2019). This requires the development of new metrics, e.g. trait measures that link to nutritional quality or cultural services such as aesthetic appeal. Applied studies could explicitly measure relevant ecosystem services, e.g. by involving stakeholders, assessing which services are most important to them, and adapting function measures to quantify these (Martín-López et al 2012, King et al 2015, Manning et al 2018). This approach, and many of the others outlined above requires inter- and transdisciplinary research involving stakeholders and researchers from other disciplines e.g. with farmers, local governments, agronomists and economists.

Large-grain studies without experimental control (cluster C)

The third cluster (C) contains BEF studies that cover large areas (from 100 m^2 to landscapes) (e.g. Larsen et al 2005, Garibaldi et al. 2013; Winfree et al., 2018). Due to the huge efforts required to manipulate diversity at a large spatial and temporal grain (Teuscher et al., 2016), such studies tend to be observational, comparative, and of low replication, although the large number of such studies has allowed for meta-~~level~~ analyses to be conducted (Lichtenberg et al. 2017). The focal study organisms also tend to be invertebrates, particularly pollinators, instead of plants. The measurement of biodiversity (e.g. species richness and functional diversity) is also often limited in these studies due to the effort required to measure it directly over large areas. As a result, it is often landscape variables, such as landscape configuration and the proportion of different land uses that are related to function, rather than diversity (e.g. Bosem Baillod et al 2017, Hass et al., 2018). These landscape properties may influence the dispersal, abundance and diversity of organisms within the landscape, and may also correlate with management factors and abiotic drivers of ecosystem function (Gámez-Virués et al., 2015; Dominik et al., 2018; Lindborg et al., 2017). As a result of these covariances, the role of biodiversity in driving ecosystem functioning cannot always be confidently ascribed (Tscharntke et al 2016).

Within this cluster, we also place remote sensing studies (e.g. Oehri et al., 2017) and national and regional correlational studies (e.g. Anderson et al., 2009). In these, biodiversity can only be measured using proxies or with presence/absence data within large grid cells (e.g. 10 x 10 km), e.g. from national monitoring schemes. These coarse biodiversity measures are then correlated with ecosystem service proxy measures such as carbon storage and recreational use. These studies often lack a strong mechanistic basis, and focus instead on how biodiversity co-varies with ecosystem services (e.g. Anderson et al., 2009, Maskell et al., 2013). Even where covariates are included and mechanistic relationships postulated (e.g. Oehri et al., 2017; Duffy et al., 2017), causal links are hard to infer due to the strong covariance between biodiversity and other drivers, and the high probability of missing, or improperly measuring, important covariates. Another common type of BEF study at this scale are those showing that functional biodiversity co-varies or differs across environmental gradients and management regimes (Rader et al., 2014, Gámez-Virués et al., 2015). While there is significant evidence that functional traits do relate to ecosystem processes and properties at landscape and national scales (e.g. Lavorel et al. 2011, Garibaldi et al. 2015, Manning et al 2015), evidence for a mechanistic link between the functional diversity of traits to the supply of ecosystem services at these scales is generally limited.

What can be transferred

As the studies of cluster C are performed in real landscapes, and as management is often conducted at large scales (e.g. by farmers or foresters), research findings from this cluster are potentially of high relevance to policy and large-scale management, e.g. via payments for ecosystem service schemes. In recent years, a number of studies have demonstrated large-scale benefits of landscapes with high diversity of crops and non-crop habitats, which support higher biodiversity (Gardiner et al., 2009; Redlich et al., 2018). These benefits include more effective pollination and biological pest control (Garibaldi et al. 2013; Winfree et al., 2018). By showing how diversity and diversification practices influence ecosystem service delivery, these practices can then be incorporated into agronomic considerations (Rosa et al., 2019) and into agri-environment policy (Garibaldi ~~e t~~ al. 2014). Studies at this scale also complement those of the other clusters by showing that biodiversity not only promotes ecosystem function and services at the plot scale but also via spillover effects into the surrounding landscape, with ecosystem service benefits including pest suppression, pollination, and bird watching potential (Blitzer et al 2012, Werling et al 2014). However, biodiversity does not always promote function at these scales. For example, natural enemy diversity does not always relate to pest abundance, nor higher crop yields (Tscharntke et al. 2016), and in some cases biodiversity does not control pests as effectively as pesticides (Samngegard et al. 2018).

Barriers to transfer and directions for future research

The observational nature of most research in this cluster means that the exact role of diversity in driving ecosystem function and providing ecosystem services at these scales is hard to ascertain. This general limitation is compounded by several other barriers which can prevent transfer to landscape management and policy. First, several processes could drive BEF relationships at landscape scales that do not operate at the smaller grain size of clusters A and B, and as a result are little acknowledged in BEF research, outside of theory (Loreau et al., 2003; Tscharntke et al., 2012; Lindborg et al., 2017). These include the spatial processes that maintain diversity, the matching between species and environmental conditions in which they perform well (Leibold et al. 2017, Mori et al 2018), and the potential for different species to provide different functions and services in different patches of the landscape, thus boosting landscape multifunctionality (van der Plas et al 2016, 2019b). The strength and role of such mechanisms clearly needs to be demonstrated. Another key problem in transferring BEF research to large scales is that landscape managers typically seek to simultaneously promote multiple ecosystem services, i.e. the multifunctionality of landscapes, not the individual functions at the plot scale (Manning et al., 2018; Kremen & Merenlender 2018). A focus on single functions is problematic if they trade-off and the components of diversity that boost some ecosystem services diminish others. For example, the maintenance of biodiversity rich habitat may add resilience to multiple ecosystem functions at the landscape scale, but also occupies land that could be used for crop production.

New research approaches are required to overcome the difficulties in identifying how biodiversity controls ecosystem functioning at large scales, and how biodiversity may be conserved and promoted to increase the supply of ecosystem services. First, to ensure that service measures are of relevance to stakeholders, we require a better understanding of which services are demanded by different stakeholders, and at which different temporal and spatial scales, so that relevant indicator variables or ecosystem service production functions can be used (Tallis 2011). A more holistic approach, which accounts for the relative demand for different ecosystem services and how this changes with socio-economic context, is therefore required, e.g. to assess how much land can be returned to a high biodiversity condition while maintaining desired levels of food production and other ecosystem services (Clough et al 2011, Kremen & Merenlender 2018, Manning et al. 2018). Such studies should also identify what drives patterns of land use and management and hence biodiversity loss, so that appropriate interventions can be identified.

To consider landscape multifunctionality and its dependence on biodiversity, multiple ecosystem services need to be scaled up in space and time, which is challenging. Some of the functions that can be measured at the plot scale can be 'linearly' scaled up, e.g. by using remote sensing proxies of diversity and functional traits, and interpolated maps, e.g. of climate and soil properties (Manning et al., 2015; van der Plas et al., 2018). Others, however, require an understanding of spatial interactions that makes their upscaling more complex, e.g. pollination and nutrient leaching (Koh et al, 2016, Lindborg et al 2017.). Furthermore, some services that operate at large scales (e.g. flood control, landscape aesthetics) cannot be predicted and scaled up from small-scale measures. Therefore, new procedures and methods are needed to quantify large-scale multifunctionality and the role of biodiversity in driving it. There have been calls for landscape-scale experiments to address these issues (Koh et al., 2009; Landis 2017). One example is the recent EFForTS project in which "tree islands" of varying size and tree diversity (0-6 species) have been planted in oil-palm clearings (Teuscher et al., 2016). Initial results indicate no economic trade-off: the islands generate yield gains which compensate for the reduced number of oil palms (Gerard et al., 2017). However, the high financial cost and/or logistical effort of such experiments means it may be more realistic to use biophysical models in most cases. Unfortunately, such models do not currently fully represent the complexity of biodiversity or its relationship with ecosystem functions and services (Lavorel et al 2017).

To understand biodiversity-landscape multifunctionality relationships, a greater knowledge of which aspects of diversity underpin different ecosystem services is also required. While knowledge exists regarding the drivers of many ecosystem service provider groups at the landscape scale (e.g. plants, birds, butterflies and pollinators, Roschewitz et al. 2005, Rösch et al. 2015, Kormann et al 2015, Grab et al. 2019), this understanding needs to be extended to other groups, including soil microbes and fauna. Similarly, understanding of how spatial biodiversity dynamics affect functions and the services they underpin needs to be extended to taxa involved in services other than pest control and pollination (Table 1). In some cases, there may be trade-offs between services, e.g. if the conditions that maximize the diversity of one taxa do not favor another (van der Plas 2019b). This research may also demonstrate that when it comes to real-world ecosystem services and landscape-level multifunctionality, biodiversity effects are not easily generalizable, but depend on the context. Thus, the rules of this context-dependency need to be identified (Allan et al 2015, Birkhofer et al., 2018, Samnegard et al 2018). Doing this will limit uncertainty; managers could be less reluctant to manage for biodiversity when the degree to which it provides ecosystem service benefits at larger scales has been clearly demonstrated. In semi-natural ecosystems the promotion of the biodiversity components underpinning ecosystem services are most likely to be achieved via management options that are simple and effective over large areas, and so the practices that would promote the desired facets of biodiversity, e.g. mowing or the introduction of selective grazers, may need to be identified.

Conclusion

A vast array of BEF studies has taught us much about the complex relationship between biodiversity and ecosystem functioning. In this article we argue that with some re-analysis and re-interpretation some of this research could be transferred to policy and management, where practitioners could use its insights to guide the diversification of agricultural and other human-dominated ecosystems, and inform the conservation of biodiversity in semi-natural ecosystems. However, there are numerous challenges to the transfer of BEF research to more applied research and practice, and we argue that these challenges differ depending on the spatial grain of the study and the degree of community manipulation. While acknowledging the differences in transferability between these clusters of BEF research may help resolve ongoing debate about relevance of BEF findings. A new generation of BEF research is also required. This would involve the merging and connecting research between the current clusters, e.g. the setup of a new generation of biodiversity experiments that bridge the gap between current BEF experiments and observational studies. These should be complemented by new observational studies which more comprehensively account for covarying factors and which better acknowledge the link between ecosystem function and ecosystem services (Table 1). It should be noted that the main knowledge to transfer from BEF research may simply be a stronger and more confident argument by conservation groups that it is important to conserve the diversity that is already present in semi-natural systems. In some cases BEF research may also show that not every species plays a positive or strong role in driving ecosystem functions, and that a small number of species dominate the supply of certain services (Kleijn *et al.* 2015). In such cases acknowledging the non-market benefits of species and returning to more traditional ethical arguments will help promote biodiversity conservation (e.g. Hill et al 2019). Finally, to make BEF research more applied, large-scale studies that utilise novel approaches to investigate the role of diversity in providing the desired ecosystem services at the landscape scale are required (Table 1). Accordingly, key considerations in applied BEF research are to acknowledge when research is fundamental or applied, and to clarify when services, rather than functions, are being considered, thus making it transparent which services and functions are focal and why, and acknowledging which stakeholder groups may benefit. In many respects, the technical solutions to the challenges addressed in this article are already being investigated. However, if the potential for BEF research to address global challenges is to be fully realized future BEF must also be transdisciplinary, and include the main stakeholders of the ecosystem collaboratively from their inception. By considering social-ecological context BEF research should be better able to demonstrate the social and economic value of biodiversity at the scales that matter to land managers and policy makers.

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Table 1. Research required to enable the real-world application of BEF research

Research need and approach	**Potential benefit to transfer**	**Examples or foundational studies**
Cluster A		
Identify mechanistic general rules governing complementary species combinations in existing biodiversity experiments	Suggested combinations of species for restoration, intercropping and crop rotation, mixed plantations ~~etc.~~	Zuppinger-Dingley et al. (2014) Brooker et al. (2015)
Demonstrate the biodiversity-multifunctionality relationship in sown or planted ecosystems, e.g. by	Could be used to design multifunctional species mixtures that provide	Baeten et al. (2019) Finn et al. (2013)

identifying mixtures which provide multiple desired services	benefits to a range of stakeholder groups	
Compare multispecies mixtures to the high performing species poor systems of current management	Without realistic comparison to current management alternative option will not be adopted	Binder et al (2018)
Perform BEF experiments with species pools that contain potentially useful and manageable species (e.g. self-sustaining mixtures)	High performing mixtures identified can be managed in a cost-effective manner	Kirwan et al (2007) Finn et al (2013)
Generate measures of stability that are relevant to managers	To show relationship between biodiversity and the stability sought by stakeholders	Donohue et al (2016) Oliver et al. (2015)
Demonstrate the cost effectiveness of multispecies mixtures compared to existing management and develop technology that increases this (e.g. multicrop harvesters)	Unless clear benefits are demonstrated diversification may not be adopted	Finger & Buchmann (2015) Blaauw & Isaacs (2014)
Cluster B		
Form general predictions of how biodiversity and other drivers of ecosystem function changes in response to global change drivers	Accurate and general estimates and predictions of biodiversity loss are the foundation of accurate and general assessments of their impacts	Bjorkman et al (2018) Grace et al (2016)
Develop mechanistic understanding	Would increase confidence	Grace et al (2016)

of biodiversity in real world systems, e.g. by using new quantitative tools to disentangle biodiversity effects	in correlational BEF relationships and allow their causes to be understood	
Systematically assess the relative role of alpha and beta diversity, functional composition, abundance and other covariates including abiotic factors and understand the feedbacks and relationships between these drivers	Would lead to more precise estimates of the relative role of biodiversity in semi-natural systems and its relationship with other factors	Allan et al (2015) Winfree et al (2015) van der Plas et al (2016)
Establish a new generation of experiments that varies the above factors, across realistic gradients	Would allow causation to be inferred for the above relationships	Smith & Knapp (2003) Manning et al (2006)
Assess the role of biodiversity in species rich communities, including that of rare species	Most diversity loss occurs between high and intermediate levels and rare species are more likely to be lost	Soliveres et al. (2016b) Klein et al (2003)
Provide statistical estimates of where different components of biodiversity play their greatest role and test these estimates	Can be used in regional and global assessments and projections of the expected impacts of biodiversity loss	van der Plas (2019a)
Explore the role BEF relationship within the context of ecosystem restoration, and link this to community assembly mechanisms	The restoration of semi-natural habitats may be more effective if a high diversity of species is used	Bullock et al. (2007)

Cluster C		
Understand the strength and role of mechanisms linking biodiversity to ecosystem function at spatial and temporal scales (e.g. species matching to site conditions, dispersal processes)	Biodiversity may play a different role at large scales to that established in experiments	Loreau et al (2003) Mori et al (2018)
Upscale ecosystem functions to large scales and link these to ecosystem services	Would allow the relationship between biodiversity, ecosystem functions and ecosystem services to be evaluated at management relevant scales	Clough et al (2016) Lindborg et al (2017) LeClec'h et al. (subm.)
Use upscaled measures to understand which taxa drive ecosystem services and disservices at landscape scales, and what factors drive the diversity of these taxa	Would allow important ecosystem service providers to be identified and managed appropriately	Van der Plas et al (2018) Winfree et al (2018)
Evaluate the role of biodiversity in driving landscape multifunctionality of ecosystem services (via upscaled measures)	Would allow the impact of biodiversity on a range of stakeholders and wider society to be communicated	Van der Plas et al (2018) Manning et al (2018)
Knowledge exchange (all clusters)		
Disseminate research findings effectively (e.g. via web tools and demonstration sites).	Non-academic approaches are required for BEF research findings to reach potential end-users users	Activities of: Forum for the Future of Agriculture (FFA) European Landowners

		Organisation (ELO) F.R.A.N.Z. Conservation evidence website RSPB Hope Farm
Work in collaboration with stakeholders to collect information on which ecosystem services are desired, at which different temporal and spatial scales, and their relative importance	This could inform applied BEF research, ensuring that it meets the needs of potential end-users	Geertstema et al (2016) Walter et al. (2017)

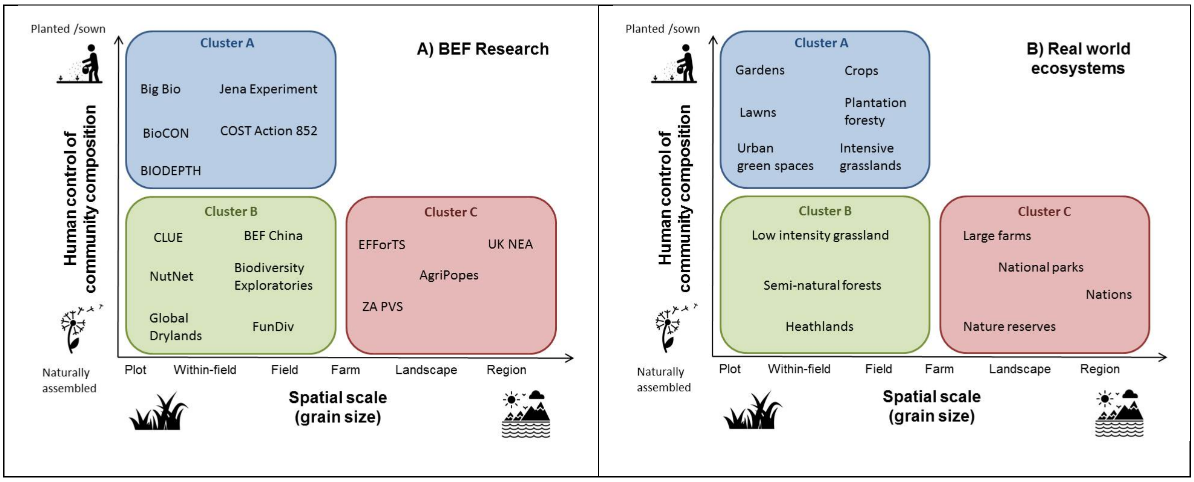

Figure 1. Clusters of BEF research and their relation to real world ecosystems. a) selected research projects, b) selected 'real-world' ecosystems. Note that, as spatial scale increases the user of research findings changes from individual local scale managers to governments and institutions and the form of transfer changes from management practice recommendations to policy change, though these are clearly interrelated Example references for studies are Jena experiment (Weisser et al 2017), BigBio (Tilman et al. 2001), BioCON (Reich et al 2001), COST Action 852 (Kirwan et al 2007), BIODEPTH (Hector 1999), BEF-China (Huang et al 2018), CLUE (van der Putten et al. 2000), NutNet (Grace et al., 2016), Biodiversity

Exploratories (Allan et al. 2015), Global Drylands (Maestre et al 2012), FunDiv (Van der Plas et al 2016), EFForTS (Teuscher et al. 2016), AgriPopes (Emmerson et al. 2016), ZA PVS (Bretagnolle et al 2018), UKNEA National Ecosystem Assessment (2011).

Figure 2. Swiss grassland diversification. In Switzerland many species rich semi-natural grasslands (left) have seen diversity decline to a more species poor state (right) due to fertilization and the sowing of low diversity mixtures. To counteract this many existing species rich sites are maintained via policy schemes and Swiss researchers have developed diversified seed mixtures suitable for a wide range of conditions that have been adopted by many Swiss farmers (Agrarforschung Schweiz 2019). This adoption is likely to be attributable to a range of factors including: a strong cultural valuation of grassland, a clear mandate of agriculture to manage sustainably (in Swiss Constitution, article 104), generous agri-environment compensation schemes for highly diverse grasslands, and a strong focus on applied grassland research that has investigated which mixes work over different time horizons (e.g. annual to permanent) and environmental conditions (moisture and elevational gradients). Finally, there is effective communication from both researchers (e.g. Agroscope) and the Swiss grassland society (AGFF, 2019), which contains many farmers as members. Photo credits. Peter Manning.