Do experiments exploring plant diversity–ecosystem functioning relationships inform how biodiversity loss impacts natural ecosystems?

David A. Wardle

Wardle, D.A. (Corresponding author, david.wardle@slu.se)

Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE901-83 Umeå, Sweden

Abstract

An enormous recent research effort focused on how plant biodiversity (notably species richness) influences ecosystem functioning, usually through experiments in which diversity is varied through random draws of species from a species pool. Such experiments are increasingly used to predict how species losses influence ecosystem functioning in 'real' ecosystems. However, this assumes that comparisons of experimental communities with low vs high species richness are analogous to comparisons of natural communities from which species either have or have not been lost. I explore the validity of this assumption, and highlight difficulties in using such experiments to draw conclusions about the ecosystem consequences of biodiversity loss in natural systems. Notably, these experiments do not mimic what happens in real ecosystems either when local extinctions occur or when species losses are offset by gains of new species. Despite limitations, this single experimental approach for studying how biodiversity loss affects ecosystems has often been advocated and implemented at the expense of other approaches; this limits understanding of how natural ecosystems respond to biodiversity loss. I conclude that a broader spectrum of approaches, and more explicit consideration of how species losses and gains operate in concert to influence ecosystems, will help progress this field.

Introduction

Although ecologists have long been aware that α-diversity (i.e. local scale species richness; hereafter 'diversity') of plant communities may have a role in determining the rates of ecosystem processes (Odum 1969; McNaughton 1977), over the past two decades this topic has attracted enormous activity. A highly popular approach to this topic has involved formal experiments that have varied the richness of taxa (usually species), often through random draws of different numbers of species from the same pool of species. Several hundreds of papers have now been published that report on experiments using such an approach (Balvanera et al. 2006; Cardinale et al. 2006, 2012), and the majority show positive relationships between species richness and certain ecosystem processes, most notably net primary productivity (NPP) and other processes that are driven by NPP. There has also been significant debate about the interpretation of these types of studies, both in terms of experimental design issues (e.g. Aarssen 1997; Huston

1997; Grime 1998), and the extent to which their results can be extrapolated to 'real world' (non-experimental) ecosystems (e.g. Srivastava & Velland 2005; Duffy 2009; Wardle & Jonsson 2010).

The results of these experimental studies on how species richness of plants and other taxa influences ecosystem processes have been presented within the context of understanding what is happening in natural ecosystems as a consequence of human-induced losses of biodiversity (Cardinale et al. 2012; Tilman et al. 2014). This is based on recognition that current extinction rates due to human activities are considerably higher than that of background extinction levels (Pimm et al. 2014), and that large losses of biodiversity are expected in the future as a consequence of human-induced global change drivers such as land-use intensification (Sala et al. 2000) and climate change (Urban 2015). Further, there have been recent attempts to use the results of experiments in which species richness has been varied as a treatment to predict the likely effects of human-induced biodiversity loss relative to those of other global change drivers on ecosystem-level processes

in non-experimental ecosystems (Hooper et al. 2012; Tilman et al. 2012).

If experiments in which species richness is varied as a formal treatment are to reliably evaluate how human-induced loss of biodiversity is impairing ecosystem process rates in non-experimental systems (as done by Hooper et al. 2012; Tilman et al. 2012), then it is essential that the behaviour of the randomly assembled communities in these experiments is indicative of how naturally assembled communities behave. Specifically, it must be demonstrated that experimental plant communities that have low species richness are analogous to natural communities from which species have been lost from the community via local extinction. I will address the extent to which this assumption is supported by the available evidence, and assess whether experiments involving manipulation of species richness are relevant to understanding on how declining global biodiversity is compromising the functioning of terrestrial ecosystems. The primary focus of this article is on plant diversity, although examples will also be used from other taxa where relevant for illustrating key conceptual points.

Do experiments show consistently declining ecosystem functioning with fewer species?

It has commonly been assumed that experimental results showing that less diverse communities perform less well than more diverse communities are directly transferrable to non-experimental systems. If the responses of ecosystem process rates to declining plant species richness were demonstrated to be similar across different types of ecosystems or groups of organisms (e.g. trophic groups) then it would be much easier to transfer the results of experimental studies to natural ecosystems. Based on the results of numerous experimental studies, it has been suggested that the responses of ecosystem processes to varying species richness are relatively consistent (e.g. Cardinale et al. 2006; Duffy 2009; Tilman et al. 2014), and two lines of evidence are often used to support this. The first is that for the pan-European BIODEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems) experiment where there was no statistically significant difference among eight field sites in the relationship between NPP and sown plant species richness (Hector et al. 1999). The second is that the meta-analysis of Cardinale et al. (2006) showed no statistically significant differences at $P = 0.05$ between species richness (of plants and other taxa) and ecosystem process rates among different ecosystem types or trophic groups (although some tests came close to significance). However, the absence of a significant effect can be due to lack of statistical power (and Type II error, not considered or tested in either study) rather than the fact the

effect is non-existent, and this is especially the case when results from disparate studies, often with very different methodologies (as is the case in this topic), are combined into a single meta-analysis.

A more powerful way of determining whether relationships between species richness and process rates vary among ecosystems is to repeat the same experiment (and apply identical methodology) across contrasting environments. In contrast to the conclusions drawn from Hector et al. (1999) and Cardinale et al. (2006), the handful of studies employing this approach provide compelling evidence that the nature of the relationship between diversity and ecosystem processes varies greatly with various environmental conditions, notably nutrient availability (e.g. Fridley 2002; Wardle & Zackrisson 2005), habitat heterogeneity (Tylianakis et al. 2008) and densities of organisms in other trophic levels (e.g. Mulder et al. 1999; Schädler & Brandl 2005). The results of such studies are also consistent with theory, which predicts that the balance between competition and resource use complementarity (one of the main mechanistic drivers of relationships between plant diversity and NPP) should be strongly impacted by both resource availability (Grime 1979) and trophic interactions (Hairston et al. 1960). If the relationship between diversity and ecosystem processes is not consistent but instead highly dependent on environmental context (and with the nature of context-dependent effects being poorly understood), then this creates considerable challenges if we are to meaningfully use the results of experimental studies to understand how and under what conditions diversity loss affects ecosystem processes in natural communities.

While the majority of experimental studies on how biodiversity affects ecosystem processes have focused on the producer subsystem, a growing number have also addressed the decomposer subsystem, by quantifying how the diversity of live plants, plant litter or decomposers affect rates of plant litter decomposition and below-ground fluxes of carbon and nutrients. The results of these studies reveal a variety of effects of biodiversity on below-ground ecosystem processes, ranging from neutral to highly positive or negative (reviewed by Wardle & van der Putten 2002; Hättenschwiler et al. 2005; Srivastava et al. 2009). This variation emerges because there are multiple mechanisms through which decomposer processes are affected by biodiversity and which can work in opposing directions (Wardle & van der Putten 2002; Eisenhauer 2012), and because the degree of coupling between the above-ground and below-ground subsystems appears to vary greatly between ecosystems for reasons that are not well understood (Bardgett & Wardle 2010). As such, strong positive effects of plant diversity on decomposer activity resulting from enhanced NPP (e.g. Lange et al. 2015), and resulting feedbacks above-ground, are only likely to emerge in those

situations where the two subsystems are closely coupled (Bardgett & Wardle 2010). Significant advances in our understanding of the drivers of this coupling are needed before we can convincingly use the results of experimental biodiversity manipulation studies to explain how below-ground processes may be affected by loss of biodiversity in nature. Such an understanding is important because of the key role of feedbacks between above-ground and below-ground biota in driving not just below-ground processes but also above-ground plant growth and thus ecosystem productivity in the longer term (Eisenhauer 2012).

One further issue is that the relationship between plant species richness and ecosystem process rates in experimental systems may strengthen over time (e.g. through increased resource use complementarity), and it has been shown that the impact of plant diversity on NPP increases with experimental duration (Cardinale et al. 2007; Reich et al. 2012). Such results have been used to suggest that studies failing to find strong ecosystem effects of biodiversity have run for insufficient time for large effects to emerge (Duffy 2009). While too few diversity experiments have been of sufficient duration to test whether this is the case, it is noteworthy that two on-going experimental studies, each set up in 1996 and each including treatments that involve biodiversity manipulation, do not find consistent evidence for plant diversity impacting plant biomass (Bezemer & Van der Putten 2007; Wardle et al. 2012). With regard to the below-ground subsystem, some experiments that have run multiple years do not find consistent effects of plant diversity on soil processes (Hedlund et al. 2003; Wardle & Zackrisson 2005). Although the available evidence suggests that while effects of biodiversity on ecosystem functioning can strengthen greatly over time, considerable variation among studies may still exist due to environmental context. This generates challenges in extrapolating the results of even long-term experiments to understanding natural systems.

Do experimental communities with varied species richness resemble natural communities?

If experimental plant communities from which species have been randomly drawn from a species pool are to be used as models of how natural communities behave, then randomly assembled communities need to resemble natural communities. This requires the assumption that low diversity communities are random subsets of high diversity communities. Yet there is abundant evidence that this is not the case (Leps 2004), an issue that is frequently overlooked. First, this assumption requires that biological communities are random assemblages of species, but it is well known from the extensive literature on plant succession that they are not, because species assemblages develop

non-randomly over time through dispersal, competition, facilitation and other biological mechanisms (Smith & Huston 1989; Walker & del Moral 2003). Second, communities that have low diversity as a result of environmental harshness or competitive exclusion consist of a highly non-random subset of the total pool that usually has a distinct set of functional traits (Leps 2004). While studies of randomly assembled experimental communities with varying species richness have played a major role in biodiversity–ecosystem function theory, they have distinct limitations for explaining how non-experimental communities behave. A related limitation is that the outcome of such experiments can be influenced to varying extents by 'sampling effect' (i.e. through species that exert disproportionate effects on ecosystem processes having a higher probability of being included in a more species-rich treatment; Aarssen 1997; Huston 1997). While it is frequently assumed that this is a legitimate biological mechanism, this requires the fundamental assumption that natural communities are randomly assembled.

While experimental studies in which species richness and composition are varied as a treatment overall show positive relationships between diversity and ecosystem processes (Balvanera et al. 2006; Cardinale et al. 2006), observational studies on natural ecosystems frequently show much weaker relationships (e.g. Wardle et al. 1997; Grace et al. 2007; Maestre et al. 2012; Soliveres et al. 2014). Various reasons have been suggested as to why experimental and observational studies exploring the consequences of species diversity often show poor agreement (Schmid 2002; Duffy 2009). However, if species richness were an important driver of ecosystem processes relative to other drivers, then diversity effects should be of sufficient strength to be detectable against background variation in those drivers (Grime 1998; Wardle & Jonsson 2010). The fact that there are several cases in which they are not detectable means that any effect of variation in diversity is likely to be of only secondary importance to variation in relation to other factors such as resources, biotic interactions and species composition (Grace et al. 2007).

The poor agreement between experimental vs observational studies could be simply because communities in many experimental studies are randomly assembled, whereas communities in non-experimental systems are not. As an example, when nutrients in an ecosystem become more abundant, plant diversity often declines, and with the community becoming increasingly dominated by a non-random subset of the flora, i.e. those species with functional traits that are related to higher productivity, higher litter quality and positive effects on nutrient fluxes (Wardle et al. 1997; Manning et al. 2006). The expected net consequence of this is increased rates of ecosystem

processes in the less diverse community, rather in the more diverse community, as found in random assembly experiments.

The issues discussed here also apply to the concept of biodiversity and multifunctionality, and to the suggestion that more diverse communities are needed to provide a wider range of ecosystem functions. Experimental studies involving random assemblages of species provide strong support for such a concept (Lefcheck et al. 2015), but there have been few tests in natural, non-random systems. Two recent non-experimental studies (Maestre et al. 2012; Gamfeldt et al. 2013) do show a statistically significant positive relationship between plant biodiversity and multifunctionality, but in one of these studies (Maestre et al. 2012) the effect of biodiversity explains less than 4% of the total variation, suggesting a much larger role of other factors. The question remains as to whether experiments in which species richness is randomly assembled are more likely to show an effect of biodiversity on multifunctionality than are naturally assembled communities in which functional trait spectra co-vary with species richness. It is well recognized that many ecosystem processes are driven by plant functional traits (albeit with different traits driving different processes), and different plant traits are frequently coordinated across species (Díaz et al. 2004; Wright et al. 2004). Such trait coordination would justify a prediction that the same plant species (and ultimately their trait spectra) are likely to drive multiple ecosystem processes, and this runs counter to the concept of multifunctionality in which different species are predicted drive different processes. To date there has been no attempt to reconcile these two opposing predictions and the extent to which they hold for non-experimental systems.

Do experimental communities with varied species richness predict ecosystem consequences of local extinction?

Two recent studies have each used the results of experiments involving randomly assembled communities to address how biodiversity loss in real ecosystems may impact on ecosystem functioning (Hooper et al. 2012; Tilman et al. 2012). Both studies concluded that decreases in species richness may have effects on ecosystem functioning that are on par with other major ecosystem drivers (e.g. drought, carbon dioxide (CO_2) enrichment, fire, invasive species, nitrogen (N) deposition), and results from these studies have been presented as evidence that biodiversity loss of the magnitude being caused by human activity has effects that are as (or even more) important as these other drivers (Tilman et al. 2014). However, there are problems with this approach.

First, in the same way that plant communities are not random assemblages of species, species are not randomly lost from plant communities (Leps 2004; Wardle et al. 2011). This is because species traits that influence the susceptibility of species to local extinction ('response traits') are often linked (either positively or negatively) to species traits that influence ecosystem functioning ('effect traits'). For example, those plant species that are the most susceptible to loss through N deposition (Manning et al. 2006) or forest harvesting (Wardle et al. 2008) also have disproportionately strong effects on both above-ground and below-ground processes. Conversely, those species that are rare or have low abundances are often more likely to become lost from the community (Thomas 1994), and those species often have weak effects on ecosystem processes (Grime 1998). Any association (either positive or negative) between 'response' and 'effect' traits in this context explains why studies involving realistic species loss scenarios often find effects of biodiversity loss that are either larger or smaller than what is often shown in random assembly experiments (e.g. Smith & Knapp 2003; Zavaleta & Hulvey 2004; Berg et al. 2015).

Second, studies such as those of Hooper et al. (2012) and Tilman et al. (2012) assume that human-induced losses of biodiversity occurring globally are being manifested at the much smaller (plot-sized) spatial scales at which biodiversity manipulation experiments are performed. However, many ecosystems are also gaining species through biological invasion and range expansion, which is homogenizing the Earth's biota and in many cases causing enhanced species richness at local and regional scales (Sax & Gaines 2003; Ellis et al. 2012). Recent studies involving long-term time-series measurements on the same pieces of land have shown no evidence of an overall (or global) decline in biodiversity at local spatial scales (Velland et al. 2013; Dornelas et al. 2014a). However, there is considerable variation among locations, and when only areas subjected to land-use alteration are considered there is evidence of some decline (Gerstner et al. 2014; McGill 2015; Newbold et al. 2015). While the interpretation of these recent studies continues to be debated (Cardinale 2014; Dornelas et al. 2014b; McGill 2015) there is little evidence that species richness is consistently declining at local spatial scales except where intensive land use and/or resource exploitation is taking place. In the absence of such evidence, local-scale experiments in which biodiversity is varied cannot effectively predict how the loss of global biodiversity currently underway is influencing ecosystem functioning. A more productive way forward would be to use local (e.g. plot) scale experiments to explore how the simultaneous losses of some species and gains of others are driving the Earth's ecosystems (Wardle et al. 2011; Mascaro et al. 2012).

One further point in relation to the studies of Hooper et al. (2012) and Tilman et al. (2012) is that if current global species richness losses resulting from human activity are sufficiently large to cause major impairment of ecosystem processes such as NPP, then this impairment should be observable at the global scale. However, although estimates of past changes in global NPP (and projections of future global NPP) are somewhat imprecise, the available evidence is that NPP globally has instead been increasing as a result of warming and increasing CO_2, and will continue to do so albeit at a decelerating rate (Ballantyne et al. 2012; Running 2012; Wieder et al. 2015). Since there is no evidence that NPP when averaged across the globe is declining despite the Earth undergoing very large losses in biodiversity, there is little evidence to support the claim that human-induced species richness loss is influencing ecosystem functioning globally to the same degree as are other global change drivers, notably climate change, CO_2 fertilization and land-use change. This may because: (i) the relationships between species diversity and ecosystem functioning is less consistent in natural ecosystems than many experiments would suggest (e.g., because in nature there is high context dependency and/or non-random assembly of communities); (ii) species losses in natural communities are non-random; or (iii) species gains through biological invasion are offsetting species losses at local and regional scales.

Conclusions and a way forward

There is significant doubt about the validity of a widely held assumption that rates of ecosystem processes in randomly assembled experimental plant communities varying in species richness can predict how biodiversity loss affects ecosystem functioning in real ecosystems. We face considerable challenges in extrapolating the results of these experiments to natural systems, because contrary to what had often been claimed, there is strong evidence of context dependency in terms of how biodiversity and ecosystem function are related. Few studies have sought to explore this context dependency and it is therefore little understood. Contrary to what is often assumed, random assembly experiments neither bear much resemblance to how natural communities are assembled, nor mimic what happens in real ecosystems when actual extinction events occur or when losses of species are offset by gains of new species through biological invasion and range expansion. There is therefore a clear need for future research to explicitly address how and why effects of biodiversity losses on ecosystem functioning vary across different ecosystems, and how species that are lost from biological communities during local extinction differ in their ecosystem effects from those that remain or are gained. While random

assembly experiments in which species richness is varied have greatly advanced theoretical understanding and are no doubt informative for addressing how ecosystems perform in managed agricultural or forestry production systems in which different numbers of species are planted, they have limitations for understanding how biodiversity loss is influencing the Earth's ecosystems in nature.

Any major scientific question is arguably best answered when a variety of approaches are used to tackle it, given that every approach will inevitably have its own strengths and weaknesses. Real progress is made when different approaches applied to the same question point to the same or similar answers. In this light, our understanding of how plant biodiversity loss affects real ecosystems has arguably been impaired because studies that have used a single approach (i.e. random assembly experiments with varied species richness) have been vigorously advocated and profiled (including via the media and multidisciplinary science journals) at the expense of all other empirical approaches. As such, many hundreds of studies have been published using this one approach, and the numbers of studies that have explicitly used alternative and arguably more realistic empirical approaches for understanding how biodiversity loss affects ecosystem functioning are fewer and have attracted considerably less attention.

One such alternative approach involves non-random removal experiments performed in natural communities (Díaz et al. 2003). These experiments have different strengths and weaknesses in relation to the random assembly approach and a higher degree of realism, but have attracted nowhere near the same amount of attention or use. Other potential approaches involve the explicit consideration of plant functional traits (Suding et al. 2008). Despite the vast and expanding recent literature on plant functional traits and functional diversity, trait-based approaches have still been employed relatively sparingly for understanding how biodiversity loss in natural systems impacts on ecosystem functioning (Díaz et al. 2013; Holzwarth et al. 2015). It is notable that at least for consumers, some of the most spectacular insights about how biodiversity loss affects ecosystems have emerged from approaches other than random assembly experiments, for example those studies that have focused on how human-induced extinctions of large mammals have transformed ecosystems (e.g., Zimov et al.1995). Notably, a recent and highly influential synthesis (Estes et al.2011) was able to provide significant insights as to how human-induced extinctions of upper level consumers have altered ecosystem properties worldwide without a single mention of the random assemblage experimental approach. There is little dispute that human-induced biodiversity loss is greatly altering the Earth's ecosystems, but our knowledge of how these effects occur is being hampered by the widespread use of

just one strongly advocated approach, without serious consideration of its limitations or of alternative approaches, in a manner that could be seen as 'confirmation bias' (Maier 2012; Velland 2014).

Finally, biodiversity loss through local extinction is the inverse of local species gain through biological invasion, so similar approaches should be applicable to understanding the ecosystem-level consequences of both processes (Wardle & Jonsson 2010). There have been enormous gains in understanding how plant biodiversity gain through invasion impacts on ecosystems because a variety of approaches (as opposed to a single approach) have been widely used, including those that directly address the issue in natural ecosystems (Vilà et al. 2011; Simberloff et al. 2013). Because species loss through local extinction and gain through invasion is occurring simultaneously, a productive way forward would be to apply approaches widely used for understanding how biological invasions affect ecosystems for addressing how biodiversity loss affects ecosystems (Wardle et al. 2011), and to explore how the concurrent gains and losses of species act in concert to determine the ways that ecosystems function (e.g., Mascaro et al. 2012).

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