

# FORUM FORUM FORUM

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

## *Biodiversity and ecosystem productivity: implications for carbon storage*

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Recent experiments have found that Net Primary Productivity (NPP) can often be a positive saturating function of plant species and functional diversity. These findings raised the possibility that more diverse ecosystems might store more carbon as a result of increased photosynthetic inputs. However, carbon inputs will not only remain in plant biomass, but will be translocated to the soil via root exudation, fine root turnover, and litter fall. Thus, we must consider not just plant productivity (NPP), but also net productivity of the whole ecosystem (NEP), which itself measures net carbon storage. We currently know little about how plant diversity could influence soil processes that return carbon back to the atmosphere, such as heterotrophic respiration and decomposition of organic matter. Nevertheless, it is clear that any effects on such processes could make NPP a poor predictor of whole-ecosystem productivity, and potentially the ability of the ecosystem to store carbon. We examine the range of mechanisms by which plant diversity could influence net ecosystem productivity, incorporating processes involved with carbon uptake (productivity), loss (autotrophic and heterotrophic respiration), and residence time within the system (decomposition rate). Understanding the relationship between plant diversity and ecosystem carbon dynamics must be made a research priority if we wish to provide information relevant to global carbon policy decisions. This goal is entirely feasible if we utilize some basic methods for measuring the major fluxes of carbon into and out of the ecosystem.

Particular, as plants are the primary avenue for ecosystem carbon uptake. studies have addressed how plant species or functional diversity may influence ecosystem-level processes, such as Net Primary Productivity (NPP).

NPP is defined as the amount of carbon retained within plant biomass, and is measured as the total amount of carbon fixed by the vegetation (Gross Primary Productivity, GPP) minus plant respiration, and losses to the soil (fine root turnover, exudation) and heterotrophs. NPP is commonly used in ecological research as an integrated measure of ecosystem functioning (Polis 1999), and also represents a key ecosystem service for humans (Vitousek et al. 1986). As a result, recent experiments addressing the relationship between plant species richness and ecosystem functioning have typically investigated plant diversity effects on net primary productivity (NPP), most commonly measured as above-ground biomass growth. However, if we are interested in the role of ecosystems in the global carbon cycle and the capability of the terrestrial biosphere to regulate future levels of atmospheric CO<sub>2</sub> levels, we must consider the net effect of the total amounts of carbon entering and leaving the whole ecosystem (Bazzaz 2001). This balance between photosynthesis and ecosystem respiration is referred to as Net Ecosystem Productivity (NEP), and is a better measure of the ability of ecosystems to mitigate human-induced increases in atmospheric CO<sub>2</sub> than NPP. The magnitude and direction of this flux represents carbon storage in the whole ecosystem over a given period of time, rather than carbon storage in plant biomass only. As more than 70% of the carbon retained within terrestrial ecosystems is found in soils (Schimel 1995), above-ground plant biomass is probably not a good estimator of NEP. As a result, more biodiversity experiments need to address carbon fluxes within the soil compartment.

The central role played by the terrestrial biosphere in the contemporary global carbon cycle has re-ignited interest in understanding what factors control the functioning of natural ecosystems (Schimel et al. 2001). Until recently, ecosystems were viewed as 'black boxes', predominantly controlled by large-scale, extrinsic factors (e.g. climate, disturbance regimes). There is now a growing realization that processes within ecosystems (intrinsic factors, e.g. community composition) could exert strong controls on these dynamics (Naeem et al. 1999, Tilman 1999). Given the rapid and accelerating rate of human-induced species losses that the planet is now experiencing (Walker and Steffen 1999, Sala et al. 2000), research has focused on the relationship between biological diversity and ecosystem functioning. In par-

In many of such biodiversity experiments, there is an implicit assumption that diversity-induced changes in NPP will influence the amount of carbon that can be stored in terrestrial ecosystems in the future (e.g. Reich et al. 2001). However, NPP could be quite a poor index for ecosystem carbon storage (Körner 2000, Schlesinger and Lichter 2001), and across ecosystems, the two might be inversely correlated (Cebrián and Duarte 1995, Cebrián 1999). Spatial and temporal variation in ecosystem productivity is often driven by changes in the activity of the soil compartment, rather than changes in plant productivity (Goulden et al. 1996, Valentini et al. 2000). Without good empirical evidence, it is premature to draw conclusions about ecosystem carbon storage from plant productivity measures.

NEP is a good measure of the total amount of carbon retained by the system over a given measurement period, but does not necessarily indicate how long this carbon will remain in the system. Soils have a finite capacity to store carbon in the longer term (Paustian et al. 2000), with the upper limit set by its clay and silt content (Hassink 1997). This limit is known as the *potential* carbon storage of a system, and is effectively fixed by these soil characteristics (Ingram and Fernandes 2001). As a result, potential carbon storage will not be altered by changes in plant community composition or diversity. Nevertheless, if changes in biodiversity persist for many generations, NEP will determine how quickly the storage potential of the soil is reached, or if it is reached at all. In fact, in today's human-dominated world, the high degree of disturbance that all natural ecosystems currently undergo means that this limit to carbon storage will likely never be reached (Schlesinger 1997). It is more relevant to ascertain how much carbon the system can retain in the medium term (known as *attainable* carbon storage; Ingram and Fernandes 2001). NEP is a direct measure of this level of carbon storage, and thus provides a more valuable measure of the ability of terrestrial ecosystems to mitigate increases in atmospheric CO<sub>2</sub> than would soil carbon storage potential. In this paper, we consider the importance of biodiversity for *attainable* not *potential* carbon storage.

Biodiversity will influence NEP (and thus carbon storage) through its impact on a suite of processes that determine the balance between GPP and both autotrophic and heterotrophic respiration (Fig. 1). NPP is just one component of the ecosystem carbon budget, but remains the focus of most biodiversity-ecosystem functioning studies. Very few studies have directly examined effects of plant diversity on many of the major carbon fluxes (but see Naeem et al. 1994). In this paper, we examine the range of mechanisms by which plant diversity could influence whole-ecosystem productivity, and hence attainable carbon storage, incorporating processes involved with carbon uptake (productivity), carbon loss (autotrophic and heterotrophic respiration), and residence time of carbon within the system (decom-

position rate). In the process, we demonstrate that if we wish to predict impacts of species loss on ecosystem carbon storage, future studies must address impacts of plant diversity on all major components of ecosystem carbon budgets, rather than NPP in isolation.

## Plant productivity

Photosynthesis is the primary pathway for the transfer of carbon from the atmosphere into ecosystems, and as such sets a limit on the amount of carbon that can be retained in ecosystems. The relationship between biodiversity and plant productivity has recently been the focus of a large number of ecological studies (summarized in Loreau et al. 2001), although most experimental work has been limited to using grassland plant assemblages. In these kinds of experiments at least, NPP is most commonly a positive saturating function of plant diversity, although the relationship ranges from linear to null (Hector et al. 1999, Loreau et al. 2001, Tilman et al. 2001). Two distinct processes combine to produce the positive relationship between plant diversity and productivity most commonly observed in experiments (Loreau and Hector 2001), although there is still considerable controversy over the relative importance of each mechanism. Sampling effects are caused when species with extreme trait values dominate the mixtures, while complementary interactions between species can cause mixtures to outperform monocultures due to resource partitioning. As relevant data exist for very few other ecosystem types (Ewel et al. 1991, Emmerson et al. 2001, Engelhardt and Ritchie 2001), particularly those with longer-lived plants, we cannot yet know the generality of these results to date.

Potentially though, if carbon inputs into ecosystems increase with increased species diversity, so too could whole-ecosystem productivity. Increased NPP will lead to increased carbon storage in both the plant biomass,

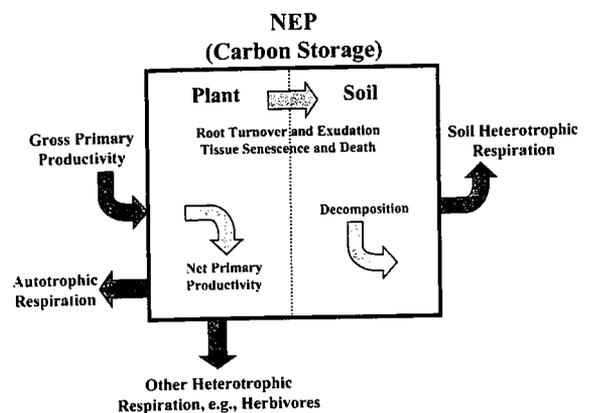


Fig. 1. Conceptual model showing the main biological components of ecosystem carbon budgets.

and the ecosystem as a whole. Storage of carbon in plant biomass could be particularly important in forests, where wood acts as a substantial carbon reservoir (Dixon et al. 1994). This sequestration in forests dominates the global terrestrial carbon sink that developed over the last decade (Schimel et al. 2001). However, changes in wood quality could uncouple NPP from carbon storage, as species favoured in more productive communities typically turn over more quickly (Phillips and Gentry 1994). Nevertheless, using plant biomass to determine NPP is only meaningful if both above- and below-ground biomass is measured. Only a small number of studies have attempted to determine root production when measuring NPP (Hooper and Vitousek 1997, Wardle et al. 1999), and in temperate systems more than 70% of the carbon in ecosystems is below-ground (Schimel 1995). But even accounting for this short-coming, the main problem with NPP is that it does not provide a reliable measure of total carbon input to a system, i.e. GPP. Ecosystem carbon inputs will not only remain in plant biomass, but will be translocated to the soil matrix via root exudation, fine root turnover, and senesced plant tissue. Very few studies have investigated plant diversity effects on GPP and the fate of fixed carbon once it has entered the ecosystem. Residence times of carbon in different ecosystem compartments vary widely (Schlesinger 1997), and could ultimately influence the productivity of the whole ecosystem. Given the shortage of studies measuring GPP and related processes, we currently do not know the extent to which plant diversity changes the fraction of carbon allocated below-ground (roots and soil), and thus uncouples above-ground plant biomass measures from GPP.

## Decomposition

### Soil organism effects

Plant species diversity will influence ecosystem-level productivity by influencing the balance between carbon inputs (plant productivity) and carbon losses (plant and soil respiration). Thus, even if increased diversity leads to increased plant productivity, these changes might not translate into increased NEP and carbon storage if respiration is also stimulated. Soil organisms are typically the primary source of heterotrophic respiration within ecosystems, and also play a key role in decomposition and mineralization of plant and soil organic matter (Swift et al. 1979). To date, impacts of plant diversity on heterotrophic activity have only been examined in a few studies. Increased diversity has been shown to increase microbial biomass and activity (Wardle et al. 1999, Stephan et al. 2000), and in some cases, these changes could translate into greater biomass further up the soil food web, e.g. earthworms and voles (Zaller and Arnone 1999, Spehn et al. 2000).

The main driver for these diversity-induced increases in soil organisms is likely to be the increased carbon supply to the soil (Mikola and Setälä 1998), as a result of greater plant biomass production (Wardle and Nicholson 1996). Theory predicts an increase in biomass or activity of higher trophic levels following an increase in a basal limiting resource (Rosenweig 1971). Thus, as many soils are carbon-limited, heterotrophic activity is typically closely tied to carbon inputs from primary production (Zak et al. 1994). However, diversity effects could go above and beyond those caused directly by increased plant productivity (Wardle and Nicholson 1996). Using an experimental diversity gradient, Spehn et al. (2000) found a positive relationship between plant diversity and soil heterotrophic activity that could not be fully explained by changes in productivity. A more diverse assemblage may provide a diet that is more balanced and more consistent through time, and thus lead to increased heterotrophic biomass. Overall, both the productivity and direct diversity effects of plant species richness on heterotrophic respiration could act to prevent increases in NPP translating into increased ecosystem-level productivity.

As well as directly affecting activity of individual soil microbial and faunal processes, plant diversity could have a large influence on the composition of the below-ground soil community, because litter inputs and root exudates determine the resource base for the whole soil decomposer food-web (Beare et al. 1992). Soil organisms have distinct functional roles within the ecosystem (Beare et al. 1995, Lavelle 1997). For example, manipulations of decomposers in freshwater systems have shown that species have different capacities for processing leaf litter, even after compensating for numerical and body size differences (Ruesink and Srivastava 2001). In turn, an altered soil community may change the processing of soil organic matter, and interact with plant diversity to influence ecosystem-level productivity (Naeem et al. 1994, 2000). In addition to direct effects from changes in food web composition, there is now growing evidence that plant diversity also influences soil community diversity. Both microbial activity and functional diversity have been shown to increase with increasing plant species richness (Stephan et al. 2000), but these effects do not always carry forward to higher components of the soil food web (Wardle et al. 1999). If plant diversity influences the variety of carbon compounds feeding the soil community, and soil organisms respond selectively to this heterogeneity, plant diversity could feed back to influence soil microbial and faunal diversity (Hooper et al. 2000).

Studies are now just beginning to examine the functional significance of altered soil biodiversity for carbon movement through the major soil carbon pools (Setälä et al. 1996, Emmerson et al. 2001). Naeem et al. (2000) found that, in freshwater microcosms, total system productivity was a complex function of both producer

(algal) and decomposer (bacterial) diversity, with a positive relationship between producer diversity and productivity only emerging when decomposer diversity was kept constant. To date, however, the small number of empirical and theoretical studies investigating the relationship between biodiversity and decomposition makes it difficult to establish how these plant-diversity induced changes in below-ground community structure will influence our understanding of the relationship between biodiversity and ecosystem productivity.

### Plant effects

The bulk of ecosystem carbon enters the soil matrix either as soluble organic matter (via rhizodeposition) or dead organic matter (plant litter). Decomposition of these pools leads to the formation of soil organic matter (SOM) (Swift et al. 1979), which can be divided into fractions that turnover more rapidly and those that comprise more persistent organic compounds (humus). The turnover rates and residence time of the different SOM fractions and the original plant litter will be a significant determinant of ecosystem carbon storage (Cebrián and Duarte 1995, Körner 2000). If plant diversity influences the size of any one of these pools, either through a change in the quantity of material entering the pool or in the turnover rate of the pool, whole-ecosystem productivity could be significantly affected.

Plant diversity impacts on litter decomposition could occur through litter mixing effects and/or microclimate effects (Hector et al. 2000, Knops et al. 2001). Experiments designed to determine the response of decomposition to different diversities of plant species litter have produced mixed results. There are examples where diversity has had no effect (Rustad 1994), where there has been a net increase in decomposition (Bardgett and Shine 1999), and where highly idiosyncratic combinations of positive and negative effects have been observed (Wardle et al. 1997). More recently, litter bag experiments conducted in the BIODEPTH (Hector et al. 2000) and Cedar Creek (Knops et al. 2001) biodiversity experiments revealed very similar results: litter decomposition was much less responsive to changes in plant diversity than NPP. More substantial positive impacts of plant diversity on NPP than on decomposition are consistent with enhanced ecosystem productivity. However, these short-term litter decomposition experiments provide a limited understanding of how plant diversity could affect ecosystem carbon storage, as they too only focus on one component of ecosystem carbon budgets. Clearly litter decomposition and SOM dynamics must be more comprehensively investigated (along with NPP) in future biodiversity-ecosystem functioning studies.

### Future approaches

Part of the reason that diversity impacts on ecosystem productivity have not been considered extensively to date is the technical difficulty with assessing ecosystem carbon storage. Above-ground NPP is a relatively straightforward ecosystem parameter to measure using basic biomass metrics, in comparison to documenting carbon fluxes into and out of the ecosystem. However, relatively simple measurements can be taken to address diversity effects on ecosystem productivity and carbon storage over the course of the experiment. If we consider the ecosystem as a 'black box', continuous or regular sampling of whole-system  $\text{CO}_2$  exchange emerges as an ideal way to investigate the magnitude of carbon uptake and loss (NEP), provided any systematic errors in sampling have been taken into account (Niklaus et al. 2000). For small plot-scale experiments, enclosure techniques using a cover-box are a particularly useful way to continuously measure canopy-level carbon flux, given their low cost and ease of operation and transport (Holland et al. 1999). For experiments using larger plots that cannot be covered by an enclosure, the eddy covariance method could be employed to continuously measure canopy-level carbon flux (Baldocchi et al. 1988). Admittedly, carbon can be lost from biological systems via a range of factors, including as leachate (e.g. dissolved organic carbon), through herbivory and as trace gas production other than  $\text{CO}_2$  (e.g.  $\text{CH}_4$ ). However, for the majority of systems,  $\text{CO}_2$  exchange will be the dominant pathway of carbon movement into and out of systems and quantification of  $\text{CO}_2$  flux will enable good estimates of NEP and ecosystem-level carbon storage.

A diverse array of other chemical and physical techniques are available to investigate whether any additional carbon will be retained in the longer term. Radio- and stable-isotopic tracers can be incorporated into systems as  $\text{CO}_2$  (Niklaus et al. 2001) or as organic residues (Nitschelm et al. 1997). Subsequent turnover and residence time of the carbon can be determined by tracking shifts in the isotope ratio as it passes through the different ecosystem compartments. Isotope techniques have been combined with physical separation methods to divide carbon into increasingly stable fractions, with the size of individual fractions used to estimate potential long-term carbon sequestration (Schlesinger and Lichter 2001). Similarly, chemical extraction can be used to separate SOM into carbon pools that turnover at different rates (Collins et al. 2000) and  $^{13}\text{C}$  nuclear magnetic resonance (NMR) spectroscopy can provide detailed chemical composition data that can be related to decomposition rates of organic matter (Hopkins et al. 1993). For many of these direct soil measures, however, experiments would have to be conducted for a number of years before a significant change in soil carbon storage could be detected, as

the sizes of fluxes are so much smaller than overall pool sizes. Measurement of whole-system CO<sub>2</sub> exchange provides an accurate measure of net carbon storage during the experiment period at least, and thus is the most feasible technique for most shorter-term biodiversity experiments.

## Conclusion

Research on the functional aspects of biodiversity now needs to move beyond effects of plant species diversity on NPP, and address impacts on whole-ecosystem productivity. NPP only provides a measure of the amount of carbon accumulating in plant biomass, but gives no indication of the total amount of carbon entering the ecosystem (GPP) or net ecosystem carbon retention (NEP). If we are interested in the ability of terrestrial ecosystems to mitigate human-induced rises in atmospheric CO<sub>2</sub>, we need to think more about controls on ecosystem carbon storage, rather than just controls on NPP. On average, more than 70% of the carbon that enters an ecosystem is retained in soil and detritus, and thus NPP does not necessarily give a good indication of the amount of carbon stored in the total ecosystem. Plant species diversity could affect carbon fluxes beyond NPP, making diversity effects on NPP a poor predictor of impacts on total ecosystem carbon retention. In this paper, we have examined how plant species or functional diversity might influence a suite of ecosystem processes that determine the balance between GPP and respiration (autotrophic and heterotrophic), and ultimately regulate whole-ecosystem productivity. While we now have a substantial amount of information on diversity impacts on plant productivity, we know much less about the relationship between biological diversity and the major processes that return carbon to the atmosphere, i.e., heterotrophic respiration and decomposition of soil organic matter. If we wish to provide information relevant to global carbon policy decisions, understanding the relationship between plant diversity and ecosystem carbon dynamics must be made a research priority. This goal is entirely feasible if we utilize some basic methods for measuring the major fluxes of carbon into and out of the ecosystem.

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