Incorporating biodiversity in climate change mitigation initiatives

Chapter · July 2009

DOI: 10.1093/acprof:oso/9780199547951.003.0011

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Biodiversity, Ecosystem Functioning, and Human Wellbeing

An Ecological and Economic Perspective

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OXFORD
UNIVERSITY PRESS

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CHAPTER 11

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11.1 Introduction

Climate change mitigation through the sequestration of carbon (C), and the protection of biodiversity have captured the attention of scientists, governmental agencies, and the public in general in the past few years. This is justifiable in view of the formidable challenges posed by them to the long-term sustainability of the Earth's life support systems (Millennium Ecosystem Assessment 2005b, IPCC 2007).

Biodiversity and C sequestration in the biosphere have seldom been considered in an integrated way, either by international conventions or by the scientific community. Biodiversity considerations have been taken into account only marginally in international initiatives and agreements aimed at mitigating the ecological impacts of climate change. The most influential of these initiatives is the Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC), which is intended to slow down the human contribution to increased atmospheric carbon dioxide concentration (http://unfccc.int/resource/docs/convkp/kpeng.pdf). This protocol was entered into force in February 2005 and has now been signed and ratified by 183 states. The Kyoto Protocol considers net C sequestration in the biosphere as one way to stabilize carbon dioxide levels in the atmosphere, and offers countries the opportunity to receive 'carbon credits' for enhancing sequestration. According to the definitions of the Marrakech Accord, climate change mitigation measures based on biological sequestration of C include afforestation, reforestation, revegetation, and forest, cropland and grazing land management (http://unfccc.int/resource/docs/cop7/13a02.pdf). However, when defining eligible C sequestration initiatives to be taken by different countries, the Kyoto Protocol explicitly excludes natural ecosystems already extant in 1990 as C sinks (http://unfccc.int/resource/docs/cop6secpart/l11r01.pdf). This is also the case with regard to the Clean Development Mechanisms (CMD, http://unfccc.int/resource/docs/2002/sbsta/misc22a04.pdf; see also Article 12 of the Kyoto Protocol) by which developed countries that emit C in excess of agreed-upon limits can obtain C offsets by investing in initiatives to sequester C and foster sustainable development in less developed countries. Here, only afforestation and reforestation qualify as eligible land use initiatives during the first commitment period of 2008–2012 (http://unfccc.int/kyoto_protocol/items/2830.php).

There is no mention of biodiversity in the main text of the Kyoto Protocol. The documents emerging from several meetings between 2001 and 2008 (Conferences of the Parties to the UNFCCC 7-13, and meetings of the Subsidiary Body for Scientific and Technological Advice, http://unfccc.int/meetings/items/2654.php) represent an advance in the sense that they incorporate biodiversity concerns. For example, the Marrakech (CoP-7), Milan (CoP-9) and Buenos Aires (CoP-10) accords, and the modalities for implementation of the CDM projects (CoP-11) explicitly state that LULUCF (land use, land use change, and forestry) and CDM initiatives must contribute to the conservation of biodiversity and sustainable use of natural resources, as well as to the promotion of C sequestration. Following the Montreal meeting (CoP 11), a request was issued to analyze the inclusion of avoided deforestation (Reducing Emissions from Deforestation and Degradation, or REDD) as part of the UNFCC activities in developing countries, either as part of the CDM next commitment period starting in 2012, or as a separate instrument designed specifically for this purpose. REDD are now an integral part of the 'Bali Road Map' (http://unfccc.int/resource/docs/2007/cop13/eng/06a01.pdf), which resulted from CoP 13. As in the case of the CDMs, the fact that the REDD initiatives should be compatible with the preservation of biodiversity is explicitly mentioned. These represent important steps forward, but biodiversity is still considered as a rather general 'side benefit' of carbon sequestration initiatives.

Academic publications (e.g. Kremen *et al.* 2000, Noss 2001, Niesten *et al.* 2002, Niles *et al.* 2002, Schulze *et al.* 2002, Sanz *et al.* 2004, Balvanera *et al.* 2005, Kremen 2005, Balvanera *et al.* 2006, Fearnside 2006b, Betts *et al.* 2008, Field *et al.* 2008) and assessment reports aimed to inform international conventions on the best ways to mitigate the effects of global change (e.g. Gitay *et al.* 2002, Díaz *et al.* 2003, Díaz *et al.* 2005, Stern 2006, Fischlin *et al.* 2007, Royal Society 2008) have stressed the importance of considering biodiversity, and analyzed the economic, social, and environmental costs and benefits of incorporating biodiversity-related criteria into C sequestration. However, in our opinion the fact that biodiversity not only has intrinsic value but could also enhance or reduce the effectiveness of C sequestration actions has not been sufficiently explored.

In this chapter we ask whether forest plant biodiversity, through its effects on ecosystem processes and especially on long-term C storage, is likely to have relevant consequences for the effectiveness of C sequestration. We first consider the theoretical background by which this could happen. Then we consider the available evidence. Finally, we make some recommendations based on this background and identify knowledge gaps and future research needs.

We refer to biodiversity as the number, abundance and identity of genotypes, populations, species, functional groups and traits, and landscape units present in a given ecosystem (Millennium Ecosystem Assessment 2005b, Díaz *et al.* 2006). In taking this broad approach, we consider species richness as just one component of biodiversity, and include other components, such as the identity and abundance of species and functional and structural traits, in our analysis, since recent syntheses (Díaz *et al.* 2005, Hooper *et al.* 2005, Díaz *et al.* 2006, Chapin *et al.* 2008) highlight the fact that composition is more important in determining ecosystem functioning than richness.

11.2 How can biodiversity affect C sequestration?

The success of C sequestration initiatives depends on how much C can be stored in the long term, which in turn depends on the net balance between C gain and C loss over long periods. It also depends on how important the C-sequestering ecosystem is perceived to be by the local stakeholders and the society at large, which in turn depends on the extent to which positive ancillary effects (such as preserved or enhanced ecosystem services other than C sequestration) can be obtained from it. This is because when stakeholders value the potential of an ecosystem to provide drinking water, food, aesthetic enjoyment, protection against natural disasters, and other services, they are more likely to protect its integrity, and therefore its C sequestration capacity, in the long term.

In this chapter we summarize the theoretical bases and some emerging evidence by which biodiversity as defined above could influence the overall success of C sequestration initiatives. We focus on path one of Fig. 11.1, and claim that biodiversity should be explicitly considered in the design of C sequestration initiatives.

It is common in international negotiations to use the term 'C sequestration' in a loose sense, to refer to the enhancement of both C stocks in and influxes into the biosphere through avoided deforestation, afforestation, reforestation, revegetation, and forest, cropland, and grazing land management. In the ecological sense, however, C sequestration refers to the maintenance or enhancement of C stocks in the biosphere. This is because large influxes can sometimes be accompanied by large effluxes, resulting in no net C accumulation. Net C sequestration occurs when the size and/or residence time of C stocks increases, due to a long-term positive balance between an ecosystem's C gains through

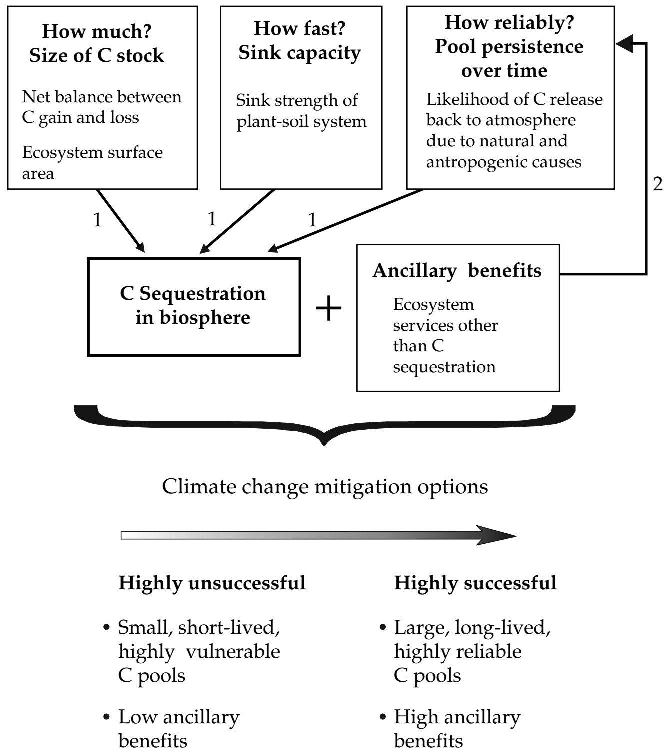

Figure 11.1 The success of climate change mitigation initiatives based on the biological sequestration of C depends on two main components: path (1), the amount and persistence of C sequestered in the plant–soil system; and path (2), the ancillary benefits provided by the C stock to humans. The positive effect of ancillary benefits is twofold. On the one hand, humans get extra benefits as well as climate change mitigation, such as regulation of water quality and quantity, soil fertility protection, traditional products, or cultural continuity ('win-win' options). On the other hand, the higher these benefits, the more likely the local communities are to preserve the C stock, thus increasing its long-term reliability.

net primary productivity and C losses through heterotrophic respiration and non-respiratory processes such as fire, harvest, and leakages of particulate, dissolved, or volatile C compounds (Catovsky *et al.* 2002, Schulze *et al.* 2002, Chapin *et al.* 2005, Schulze 2005). If biodiversity has the potential to affect C gain through productivity, or C loss through respiration and non-respiratory processes, then it follows that it should influence both the gross and the net C sequestration capacity of ecosystems. In this contribution, we use the term C sequestration (i.e. C storage) in the ecological sense, as a positive long-term change in, or maintenance of, C stocks. We refer to C influxes into the biotic system as C uptake or C capture.

Different theoretical backgrounds and some emerging evidence suggest that different components of biodiversity (species and genotype composition, number and spatial arrangement) differ in their potential to modify the magnitude, rate, and long-term permanence of the biosphere's C stocks and fluxes. Therefore, biodiversity consideration could be an integral part of the design and implementation of policy and management actions aimed at enhancing the long-term C sequestration capacity as well as the overall ecosystem-service value of primary, managed, and planted forests.

11.2.1 C sequestration predictions based on different theoretical approaches

How could biodiversity affect C sequestration in primary, managed, or planted forests? At present, there are three main theories leading to different predictions. These theories are the *neutral hypothesis*, the *mass ratio hypothesis*, and the *niche complementarity hypothesis*. We distinguish the neutral hypothesis from the other two because species differences play no role in it. Life history tradeoffs between species underlie both the mass ratio and niche complementarity hypotheses, but the first proposes that species influence ecosystem functioning according to their traits and in direct proportion to their relative abundance whereas the other also takes species interactions into account.

11.2.2 The neutral hypothesis

The Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001) predicts that diversity can be maintained with random, neutral drift in species abundances so long as the evolution of new species can balance stochastic extinctions. Within the context of the links between biodiversity and C sequestration, the neutral hypothesis acts as a useful 'nothing happens' model. The neutral hypothesis assumes that individuals of all species have equal *per capita* probabilities of recruitment and mortality. On the surface the theory may seem to predict that all species are equal, but that is only the case for the recruitment and mortality rates, and functional traits are not explicitly considered. An attempt to reconcile neutral theory with niche theory proposes that species achieve equal *per capita* rates of recruitment and mortality by different resource allocation tradeoffs (Hubbell 2001: Chapter 10). However, the relative abundance of species is random with respect to their traits. If C storage is determined by the traits of species then under a neutral model, the sequestration capacity of forests will vary randomly over time along with neutral drift in the relative abundances of species.

11.2.3 The mass ratio hypothesis

According to the mass ratio hypothesis (Grime 1998), resource dynamics at any given time in an ecosystem strongly depend on the structural and functional characteristics of the dominant (i.e. most abundant) primary producers, and ecosystem functioning should be strongly affected by their life history tradeoffs. Therefore the total C stock of an ecosystem, its sink strength (the rate of change of the stock), and its residence time (the time that C will remain sequestered in the system) should strongly depend on the functional attributes of the dominant plants, as well as on climate and soil nutrients (Fig. 11.2). The traits of the dominants should strongly influence C uptake via net primary productivity and C loss via decomposition and disturbance. Fast acquisition of C per unit of leaf biomass or leaf area and long-term conservation of standing biomass are not expected to be maximized at the same time. This is because, across major taxa and biomes, there should be a tradeoff between a suite of attributes that promote fast C and mineral nutrient acquisition and fast decomposition, and another suite of attributes that promotes conservation of resources within well-protected tissues and slow decomposition (Grime 1979, Hobbie 1992, Cornelissen *et al.* 1999, Aerts and Chapin 2000, Díaz *et al.* 2004, Wright *et al.* 2004). The former, acquisitive, suite includes attributes such as leaves that are nutrient-rich, palatable, and short-lived, and often wood of low density. This suite is more common in light-demanding early-successional plants that act as pioneers after disturbance (Coley 1983, Pacala *et al.* 1996, Cornelissen *et al.* 1999, Ellis *et al.* 2000, Ter Steege and Hammond 2001, Laurance *et al.* 2006), and leads to shorter C and nutrient residence time in the ecosystem because of their short leaf lifespan and fast litter decomposition rates (DeAngelis 1992, Hobbie 1992, Aerts 1995, Wardle *et al.* 2004a). The latter, conservative, suite of traits includes leaves that are nutrient-poor, unpalatable, and long-lived, and often dense wood. This suite is more common in late-successional plants, which in forests include mostly disturbance-intolerant species (especially during ecosystem retrogression or decline, Walker *et al.* 2001, Wardle *et al.* 2004b); these species can increase C storage and mineral nutrient residence time as a result of their long leaf lifespan and slow litter decomposition rates. As a consequence of the existence of these suites of strongly associated attributes, there is a tradeoff at the ecosystem level between short-term C assimilation rate and long-term C storage. Within forest ecosystems, many forest types are successional mosaics where early- and late-successional patches coexist as a result of natural die-off events or, more commonly, small (e.g. tree fall) and large (e.g. forest fires) disturbance events (Denslow 1987, Crews *et al.* 1995, Pacala *et al.* 1996, Richardson *et al.* 2004). Early-successional and late-successional patches are dominated by acquisitive and conservative species, respectively, leading

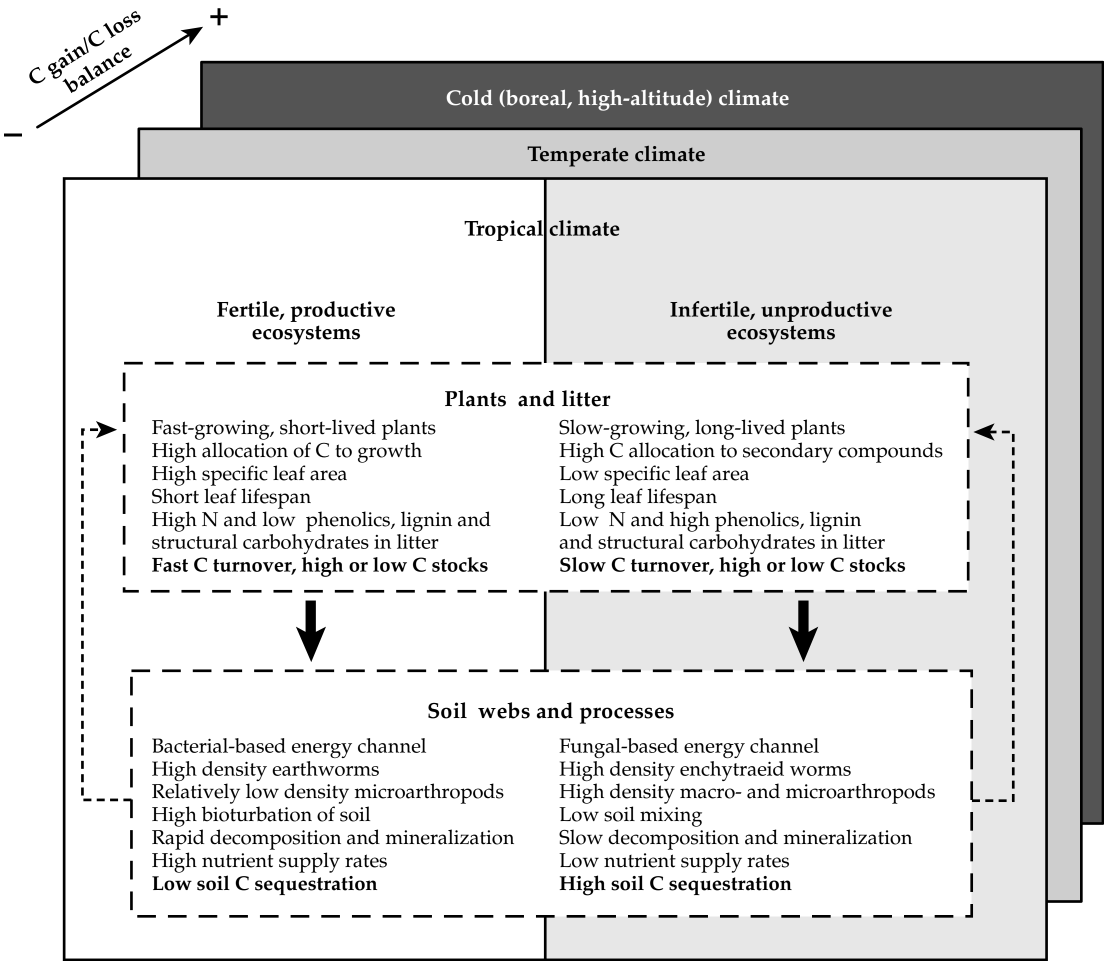

Figure 11.2 The traits of plants, especially dominant plants, strongly influence C and mineral nutrient cycling and thus C sequestration capacity in different ecosystems. Plant traits serve as determinants of the quality and quantity of resources that enter the soil and the key ecological processes in the decomposer subsystem driven by the soil biota. These linkages between belowground and aboveground systems feed back (dotted line) to the plant community positively in fertile ecosystems (left) and negatively in infertile ecosystems (right). C sequestration is highest in infertile conditions because decomposition is more impaired than net primary productivity by infertility and in colder conditions because decomposition is impaired more than net primary productivity by low temperatures (Derived from Wardle *et al.* 2004a).

to a differentiation in ecosystem processes between patches of different successional age. We should note here that while the mass ratio hypothesis describes the dominance of these strategies within patches, the landscape scale diversity between patches represents a form of niche complementarity (see below).

The structural and physiological traits of the dominant plants can also influence the probability of disturbances such as fire, wind-throw, and episodic herbivory, that are major avenues of C loss from ecosystems (Laurance 2000, Knohl *et al.* 2002, Lavorel and Garnier 2002, Chapin 2003, Pausas *et al.* 2004, Gough *et al.* 2008), and have important consequences for the long-term success of C sequestration initiatives. As well as this indirect effect through C sequestration capacity, the structural and phenological attributes of vegetation cover over large areas can affect climate directly. Functional traits of the dominants, such as leaf lifespan, growth form, root depth, and stomatal conductance affect albedo, roughness, and evapotranspiration. Through these biophysical feedbacks, the functional and structural composition of land patches can influence climate at the local, regional, and even trans-regional scale, depending on the land area covered by each vegetation type (Chapin *et al.* 2000a, Chapin *et al.* 2000b, Thompson *et al.* 2004, Chapin *et al.* 2005, Betts *et al.* 2008, Chapin *et al.* 2008). Recently, Körner (2005) has summarized the variety of functional traits in temperate and boreal tree species and their possible ecosystem-level implications, but a similar exercise has not yet been carried out for tropical and subtropical ecosystems.

Ecosystems consist of not just a producer but also a decomposer subsystem, and C sequestration is determined not just by ecosystem C gain (driven by net primary productivity, or NPP) but also by C loss (driven by decomposition). Thus, whether or not C accumulates in soils is driven to a large extent by the difference between C input to the soil (through litterfall, dead root production, and rhizosphere release) and C loss from the soil (through decomposition and respiration). Although decomposition at local (within-stand) scales is determined largely by litter quality (and hence the traits that drive litter quality), the linkages between aboveground (producer) and belowground (decomposer) communities are often relatively weak (Hooper *et al.* 2000, Wardle *et al.* 2004a, Hättenschwiler 2005). Thus decomposition rates need not respond to ecological gradients (e.g. succession, climate, diversity) in the same direction or to the same extent as does NPP. For example, decomposition is promoted by temperature more than is NPP, leading to reduced soil C sequestration at higher temperatures (Anderson 1991) and decomposition rates may decline across successional gradients while NPP is increasing, leading to rapid soil C accumulation (Wardle *et al.* 2004b). Further, plant species that produce high-quality litter may induce a ‘priming effect’ that accelerates the losses of native organic matter in the soil and thus promotes net ecosystem C loss (Jenkinson 1971). This may also explain why in some situations an increase in NPP is not matched by an increase in the amount of C stored in the soil (Fontaine *et al.* 2004), and may have important, though largely unrealized, consequences for soil C persistence and hence ecosystem C sequestration. Conversely, increasing domination of the plant community by plant species that are unproductive but contain high amounts of recalcitrant lignin and polyphenol compounds in their litter (such as can occur during ecosystem retrogression) can contribute to greater retention of C in the soil even when NPP is declining (Wardle *et al.* 2003a) (Fig. 11.2).

Tree species (or forest vegetation types) can differ markedly in the extent to which they promote sequestration of soil C (e.g. Jobbagy and Jackson 2000, Rhoades *et al.* 2000, Resh *et al.* 2002, Matamala *et al.* 2003, Russell *et al.* 2004), in a large part because they differ in their effects on the balance between C gain and C loss. For example, N-fixing trees will often accumulate more soil C than non-N-fixing trees (Resh *et al.* 2002). Systems dominated by slow-growing tree species that produce well-defended leaves (and hence poor litter quality) frequently promote substantial soil C accumulation relative to tree systems dominated by plants that grow rapidly and produce litter of high quality (Wardle *et al.* 2003a). The effectiveness of C sequestration initiatives depend on the magnitude and accumulation rate of soil C stocks, as well as the persistence of these stocks. Soil organic carbon (SOC) can be accumulated in short-lived pools, such as the microbial and labile pools (mean residence time of < 5 years), and long-lived pools in which SOC is protected by association to colloidal materials and the formation of stable micro-aggregates or recalcitrant compounds (mean residence time of thousands of years) (Lal 2005); tree species affect both of these pools. Dominant plant species have a clear influence on short-lived pools through root output and litter, and longer-lived pools through their litter quality (Wardle *et al.* 2003a), although their capacity to influence longer-lived pool is not always clear (Lal 2005, Jandl *et al.* 2007). Shallow rooting coniferous species tend to accumulate SOC in the forest floor, but they will sometimes accumulate less in deeper layers than comparable deciduous trees that often have deeper, more ramified roots. This is presumably in part due to the effective way in which root growth and subsequent root death can directly result in incorporation of organic matter inputs beneath the soil surface (Jobbagy and Jackson 2000, Trumbore 2000, Vesterdal *et al.* 2002).

The mass ratio hypothesis does not deny that less abundant species can sometimes play a major ecosystem role or face similar life history tradeoffs to those of abundant species (Grime 1998, Eviner and Chapin 2003, see below), but puts the emphasis on the functional composition of local *dominants* (Nilsson and Wardle 2005, Wardle and Zackrisson 2005). The niche complementarity hypothesis, in contrast, highlights the functional *differences* between coexisting species. These hypotheses are not mutually exclusive, and both processes can be operating in the same system (Loreau and Hector 2001, Fox 2005b, Potvin and Gotelli 2008). Many of the differences in life history traits reviewed above with regard to the mass ratio hypothesis may also be relevant to the discussion of niche complementarity that follows.

11.2.4 The niche complementarity hypothesis

This hypothesis is based on the idea that a greater range of physiological, structural, and phenological traits represented in the local community provides opportunities for more efficient resource use in a spatially or temporally variable environment (Trenbath 1974, Vitousek and Hooper 1993, Tilman *et al.* 1997c). This hypothesis is also compatible with the existence of trait tradeoffs, and indeed such tradeoffs are the basis for niche differences between species. But here there is less emphasis on the tradeoffs of the dominants as major drivers of ecosystem properties. When species show complementary niche differences it is likely – but not automatic (Hector 1998, Hector *et al.* 2002) – that a mixture of species may show greater overall resource uptake and rates of ecosystem processes than the same species grown in monoculture. Niche complementarity may relate to resource use, but mixtures may also perform better if rates of attack by natural enemies – either pests or pathogens – are higher in monocultures, in low-diversity patches, or near parent trees (e.g. Janzen 1970). Less abundant species are often minor players in ecosystem resource dynamics (Grime 1998) but may play an important role as a group, for example through ecosystem engineering (Jones *et al.* 1994), through keystone species effects (e.g. plant species that form mutualisms with nitrogen-fixing bacteria, Vitousek and Walker 1989), and through participating in complex indirect interactions (Eviner and Chapin 2003). Non-abundant species might be important in providing an insurance effect (a type of temporal niche complementarity) that helps sustain ecosystem functioning in the long term, particularly in a changing environmental context (Walker 1995, Walker *et al.* 1999, Yachi and Loreau 1999). There are few examples of insurance effects in the literature and it is therefore still too early for a formal assessment of their strength and occurrence.

The role of genetic differences between populations or genotypes of the same species in natural ecosystems has been little studied. In the case of herbaceous communities, Joshi *et al*. (2001) found that the performance of different genotypes was always best in the sites from which they were sourced, and Booth and Grime (2003) reported that communities composed of genetically uniform populations appear to be more variable in canopy structure, and to lose more species over time, than communities composed of genetically heterogeneous populations. Reusch *et al*. (2005) showed that genotypic richness of the cosmopolitan seagrass *Zostera marina* enhanced biomass production despite near-lethal water temperatures due to extreme warming across Europe. Crutsinger *et al.* (2006) showed that increasing population genotypic richness in the old-field herb *Solidago altissima* determined arthropod diversity and increased above-ground net primary productivity. However, it is difficult to know how general these patterns are, and whether they apply to woody ecosystems. Genetic variability among spatially separated populations of the same tree species has been shown to be an important driver of litter quality and ecosystem processes such as decomposition, herbivory and nutrient cycling (Treseder and Vitousek 2001, Whitham *et al.* 2003, Schweitzer *et al.* 2004, Schweitzer *et al.* 2005b), but experimental evidence on the effects of tree intraspecific genetic richness on ecosystem processes is still lacking (Hughes *et al.* 2008). Indeed, most of the evidence of the positive effects of high species and genotypic richness comes from the field of subsistence agriculture and forestry practiced by traditional peoples (Pretty 1995, Altieri 2004). This diversity is often lost during the process of selection for the production of high-yielding varieties. Therefore the possibility exists that the loss of inter- and intra-specific genetic variation could also lead to instability of plantations and other managed woody ecosystems in the face of a changing environment.

As for processes related to C loss, there are now a number of litter-mixing studies that collectively suggest that generally plant species composition of litter rather than its richness plays an important role in decomposition and nutrient cycling rates. Although the additive effects of species richness on litter decomposition cannot strictly be considered a niche complementarity effect in the sense of complementarity of resource use, they are discussed here because they involve 'richness-related' effects, as does the niche complementarity hypothesis. Litter mixing studies have found litter species richness to exert generally idiosyncratic or weak effects on litter mass loss (e.g. Wardle *et al.* 1997a, Bardgett and Shine 1999, Hector *et al.* 2000, reviewed by Gartner and Cardon 2004), while plant species richness has generally been found to exert weak or neutral effects on soil processes (Chapman *et al.* 1988, Hooper and Vitousek 1998). Further, it has been shown experimentally that addition of a greater richness of C substrates to the soil (such as might be expected in a more species-rich plant community) did not exert strong or consistent effects on C loss rates from soil, or on soil C storage (Orwin *et al.* 2006). However, in instances in which NPP is promoted by plant species richness, it is likely that decomposition rates would be less unresponsive, in which case greater C sequestration would be expected over time. The mechanistic basis through which plant richness might affect soil processes is relatively poorly understood. However, the available evidence suggests that plant species richness is not a powerful driver of soil decomposer richness (Hooper *et al.* 2000) and that decomposer richness is not a major determinant of soil process rates such as decomposition or nutrient supply rates for plants (Laakso and Setälä 1999, Setälä and McLean 2004, Hättenschwiler *et al.* 2005).

11.2.5 Where does the available evidence stand and what else do we need to know?

In summary, the predictions of these different hypotheses for the incorporation of biodiversity in C sequestration initiatives vary markedly. Taken to an extreme, the mass ratio hypothesis predicts that C storage would be maximized by planting a monoculture of the species with the combination of traits (stature, lifespan, timber density, decomposition rate, resistance to fire, wind-throw, and pests) that produces the highest species specific C storage for a given area. The niche complementarity hypothesis predicts that C storage will be impacted by interspecific differences among coexisting species, in terms of resource use and tolerance to biotic and abiotic factors. It also predicts that it may be possible to increase C storage by planting complementary mixtures of species, sets of species with known mutually facilitative effects, and/or ensuring that a mosaic of late- and early-successional patches is kept (e.g. Caspersen and Pacala 2001). Finally, the neutral hypothesis predicts that the C storage capacity of natural forests will vary randomly with stochastic shifts in species abundances. In plantations it may be possible to influence C storage by controlling the recruitment stage, for example by increasing seed or seedling input of species that are good at sequestering C but are poor recruiters.

The three hypotheses all stem from strong theoretical developments and are all supported by empirical evidence to varying degrees in forested systems. Most of the experiments from which this evidence is derived were not originally designed to test these hypotheses. Moreover, there is an important body of results of experiments specifically designed to test the effect of biodiversity (and most commonly species richness) on the functioning of grasslands (reviewed in Loreau *et al.* 2001, Díaz *et al.* 2005, Hooper *et al.* 2005) but there are few corresponding experimental studies in woody ecosystems, which may not necessarily behave in similar way to herbaceous ecosystems.

Table 11.1 provides an overview of recent studies of the role of different components of plant biodiversity in C gain and loss of forest ecosystems. They include primary forests, traditionally managed forests, and commercial and experimental plantations. Our synthesis, which is intended to be illustrative rather than exhaustive, reflects the scarcity of published studies involving woody plants. This is true for all continents, but particularly dramatic in Latin America, Africa, and Asia, precisely where most remaining high-diversity forests are located. There have been some studies that can be interpreted in the light of the mass ratio or niche complementarity hypotheses to varying degrees. As for the neutral hypothesis, we found no study directly linking it with the way in which biodiversity could affect ecosystem processes. According to the original authors' interpretation of their own results (Table 11.1, third column) there seems to be more support for the mass ratio hypothesis than for the niche complementarity hypothesis, in the sense that the authors conclude that composition (the presence of certain tree species) appears to play a more important role than species richness. However, compositional differences could arise from either mass ratio or niche complementarity effects or some combination of the two (Loreau and Hector 2001). Distinguishing the relative contributions of these two mechanisms will require future studies that are explicitly designed to discriminate among the two classes of causes. Evidence for relationships between species richness and stability of forests and plantations is mixed. It follows that particular attention should be paid to the identity of the species chosen for afforestation, reforestation and rehabilitation projects, with the actual richness of species planted taking second place. However, (1) positive effects on ecosystem functioning are often found in mixtures of two or more species compared to monocultures; (2) virtually all the reported studies were not specifically designed to distinguish between the three different hypotheses, and the patterns observed may fit more than one of them (e.g. Chave 2004, Volkov *et al.* 2005); and (3) mass ratio, niche complementarity, and neutral hypothesis mechanisms may all be acting simultaneously (e.g. Potvin and Gotelli 2008).

An experimental test of the neutral hypothesis through the removal of dominant species has recently been performed for intertidal communities (Wootton 2005), but the feasibility of this approach for use in other systems is unclear. Experiments to definitively establish the relative importance of the mass ratio and niche complementarity mechanisms for determining ecosystem properties in forests will ideally require the establishment of monocultures and mixtures of all component species under the same environmental and management conditions (e.g. Redondo-Brenes and Montagnini 2006, Potvin and Gotelli 2008). This may be practical for species-poor ecosystems (e.g. boreal forests), but it quickly becomes unfeasible if one is to incorporate even a fraction of the high richness of tree species characteristic of many tropical forests. We also emphasize that experimental approaches of this type are not the only way to formally test for the role of biodiversity in ecosystem functioning, and ideally the results of such studies should be considered alongside other approaches that have recently been employed to test how biodiversity affects forest C sequestration, such as simulation- and modelling-based approaches (Bunker *et al.* 2005), field removal experiments (Díaz *et al.* 2003, Wootton 2005), observational studies using well characterized gradients of plant diversity (Wardle *et al.* 2003a), and forestry projects that incorporate diversity components into their design (i.e. 'enrichment planting', e.g. Evans and Turnbull 2004). In the end, even being able to successfully distinguish between the relative importance of mass ratio, niche complementarity, and neutral hypothesis effects may not necessarily be crucial to the practical purposes of C sequestration, especially as these hypotheses are not all mutually exclusive. For example, experimenting with mixtures that contain non-random combinations of species (such as those that represent traditional mixtures), or maximize key ecosystem services like C sequestration plus food production, or are the most economically and socially feasible in each region, might make more practical sense than incorporating all the possible mixtures of component species within the experimental design.

Table 11.1 A summary (representative rather than exhaustive) of studies published during the last 13 years on the effects of different components of biodiversity on C sequestration through impacts on C gains or losses in woody ecosystems.

Ecosystem type and location	Main biodiversity component involved	Findings	Source
C gain			
Experimental plantations of fast-growing tropical tree species *Hyeronima alchomeoides*, *Cedrela odorata*, and *Cordia alliodora*; each species grown alone and with two perennial, large-stature, monocots (*Euterpe oleracea* and *Heliconia imbricata*)	Species and functional group richness	Ecosystem productivity and resource capture were increased when the monocots were grown with *C. odorata* and *C. alliodora*, but not with *H. alchomeoides*	Haggar and Ewel (1997)
Boreal forest trees and understorey vegetation on Swedish lake islands	Species and functional group richness	Species-rich islands less productive at large spatial scale (between islands) because more productive species dominate on less diverse islands; some evidence of greater understorey species richness promoting overall forest productivity within islands	Wardle *et al.* (1997), Wardle *et al.* (2003), Wardle and Zackrisson (2005)
Young plantations of four indigenous tree species: *Hieronyma alchorneoides*, *Vochysia ferruginea*, *Pithecellobium elegans*, and *Genipa americana*, growing in mixed and pure stands at La Selva Biological Station, Costa Rica	Species richness and identity	Total tree biomass production rate of the mixture was not significantly higher than that of the most productive monocultures	Stanley and Montagnini (1999)
Stand productivity in USA Forest Inventory and Analysis database	Species richness	Positive correlation between tree species richness and stand productivity, especially when comparing monocultures vs. mixtures of two or more species; variations in abiotic factors not considered	Caspersen and Pacola (2001)
Stand biomass in global forest dataset	Species richness	Forest stand biomass not associated with tree species richness	Enquist and Niklas (2001)
Experimental plantations of three native tree species, *Hyeronima alchoreoides*, *Cedrela odorata*, and *Cordia alliodora*, in monoculture and in mixtures with the palm *Euterpe oleracea* and the giant perennial *Heliconia imbricata*, in Costa Rica Atlantic lowlands	Species richness and composition and functional group richness	Tree species richness influenced ecosystem nutrient use efficiency in tree-only stands. Aboveground net primary productivity after four years was significantly higher in polycultures than in monocultures of *C. odorata*, and *C. alliodora*, but not in the case of *H. alchomeoides*. The presence of the additional life forms increased nutrient uptake and uptake efficiency, but only in some systems and years Although species and life forms exerted considerable influence on ecosystem nutrient use efficiency, this was most closely related to soil nutrient availability	Hiremath and Ewel (2001)
Stand productivity of boreal forests dominated by *Betula* spp., *Picea abies* and *Pinus sylvestris*, under the same environmental conditions and management	Species richness and composition	Mixtures of *Betula* spp. and *P. abies* more productive than *Picea* monocultures, but mixtures of *Betula* spp. and *P. sylvestris* were less productive than *P. sylvestris* monocultures; species richness effect significant only at early successional stages	Frivold and Frank (2002)

Long-term experimental comparison of different agroforestry systems in Brazilian Amazonia; peach palm (*Bactris gasipaes*) for fruit and heart-of-palm production, cupuaçu (*Theobroma grandiflorum*), and rubber (*Hevea brasiliensis*) planted n multistrata mixtures and in monocultures, also compared with adjacent primary rainforest and 14-year old secondary forest	Species richness and composition	Multistrata agroforestry system showed more accumulation of above- and belowground biomass than cupuaçu, rubber, or peach palm for heart-of-palm, but less than peach palm for fruit Secondary forest accumulated 50%, and primary forest likely 500% more total biomass than the most productive plantation	Schroth *et al.* (2002)
Wood production in Catalonian forests with different degrees of species richness, dominated by *Pinus sylvestris* or *Pinus halepensis*	Species richness	In *P. sylvestris* forests wood production was not significantly different between monospecific and mixed plots. In *P. halepensis* forests wood production was greater in mixed plots than in monospecific plots. No significant effect of species richness when environmental factors were considered.	Vilà *et al.* (2003)
Experimental plantations of three native tree species, *Hyeronima alchoreoides*, *Cedrela odorata*, and *Cordia alliodora*, in monoculture and in mixtures with the palm *Euterpe oleracea* and the giant perennial *Heliconia imbricata*, in Costa Rica Atlantic lowlands	Species composition and functional group richness	Light particulate organic matter C and soil C:N ratio were significantly higher, and total soil organic matter C was slightly higher, under *H. alchoreoides*, as compared to under the other two tree species Functional group richness had a positive effect on total and light/particulate soil organic matter as compared to monocultures of *C. odorata* and *C. alliodora*, but not in the case of those of *H. alchoreoides*.	Russell *et al.* (2004)
Litter production in Catalonian traditionally managed forests	Species richness, species and functional trait composition	Litter mass larger in 2–5 species mixtures than in monospecific stand. In mixed forests, identity of trees determined whether litter stocks increase with tree diversity.	Vilà *et al.* (2004)
Simulation study of the magnitude and variability of aboveground C sequestration in 18 scenarios of tree species extinction within a species-rich tropical in Panama	Species richness and functional trait composition	Different trait-based scenarios (e.g. order of extinction determined by wood density, height, growth rate, drought tolerance, also a random extinction scenario) resulted in strong differences in magnitude and variability of C stocks	Bunker *et al.* (2005)
Long-term tree-planting experiment, established in 1955 in NW England; *Quercus petraea*, *Alnus glutinosa*, *Pinus sylvestris* and *Picea abies* planted in monocultures and in 2-spp mixtures	Species richness and composition	All mixtures involving *Pinus sylvestris* showed more growth in pure stands of either species; *A. glutinosa* mixtures not involving *P. sylvestris* did not outperform monocultures, *P. abies*/*Q. petraea* mixture showed less growth than monocultures	Jones *et al.* (2005)

(Continues)

Table 11.1 (*continued*)

Ecosystem type and location	Main biodiversity component involved	Findings	Source
Review of the 20th century forestry literature with emphasis on commercial trees in the temperate and boreal zones	Species and functional group richness and composition	Increased productivity in mixtures of species with different spatial, phenological or successional niches (e.g. *Larix*/*Picea*, *Quercus*/*Betula*, *Pinus*/*Picea*, *Pinus/Betula*) Some mixtures (e.g. *Picea abies*/*Betula pendula*) sustain production over a larger range of densities than monocultures and are thus more tolerant to risks	Pretzsch (2005)
Natural and seminatural forests, plantations and secondary woodlands in the Ecological and Forest Inventory of Catalonia (IEFC), including 95 tree species	Species richness, species and functional trait composition	Stemwood production increased from single-species to 5-species stands, but stand age and richness were negatively correlated Species richness had a significant positive effect on stemwood production in stands dominated by sclerophyllous species (e.g. *Quercus*, *Arbutus*), and low-productivity conifer stands, but not deciduous species stands in humid or warmer climates	Vilà *et al.* (2005)
Experimental mixed plantations of native trees *Balizia elegans*, *Callophyllum brasiliense*, *Dipteryx panamensis*, *Hyeronima alchorneoide*, *Jacaranda copaia*, *Terminalia amazonia*, *Virola koschny*, *Vochysia ferruginea* and *Vochysia guatemalensis* in Costa Rican tropical rainforest Monocultures were compared to 3-species mixtures, all of them consisting of one fast-growing sp., one slow-growing sp., and one legume, to keep functional richness as constant as possible	Species richness	Although some individual species were more productive in mixtures than in monocultures, none of the mixtures showed significantly higher growth or C storage than the monocultures of the most productive species involved in each mixture	Redondo-Brenes and Montagnini (2006)
More than 5000 permanent forest plots in the National Forest Inventory of Spain in the Catalonia region, including 51 tree species, growing in monocultures and in 2- to 5-species mixtures	Species richness, functional group richness and identity	Stemwood production was positively associated with tree species richness and with functional group identity (deciduous forests were more productive than coniferous or sclerophyllous forests). Functional group richness did not significantly explain stemwood production once the effects of environmental and structural variables were taken into account	Vilà *et al.* (2007)
Experimental plantations of native tropical trees representing a range of relative growth rate (*Cordia alliodora*, *Luehea seemannii*, *Anacardium excelsum*, *Hura crepitans*, *Cedrela odorata*, and *Tabebuia rosea*) in monocultures, and 3- and 6-spp. plots, in Central Panama	Species richness and composition	Plot biomass (estimated from basal area) did not differ between mixtures and monocultures or among mixtures. There was a significant species richness effect on growth, attributed to complementarity, in the 3-species mixtures as compared to monocultures, but there was no significant effect in 6-species plots. Mortality was strongly dependent on species identity, and independent of species richness. Overall, there was a positive complementarity effect (using the additive partitioning method of Loreau and Hector 2001) of species richness on plot biomass and a negative selection effect, resulting in no net species richness effect	Potvin and Gotelli (2008)

C loss			
Boreal forest trees and understorey vegetation on Swedish lake islands	Species and functional group richness	Species-rich islands supported less soil respiration, microbial biomass and decomposition at large spatial scale (between islands), contributing to net C sequestration in the soil Some evidence of greater understorey species richness promoting these processes within large (but not small) islands Differences among islands in belowground processes and C sequestration are explicable by traits of dominant plant species but not species richness	Wardle *et al.* (1997), Wardle *et al.* (2003), Wardle and Zackrisson (2005)
Damage by beetle *Phratora vulgatissima* and rust *Melampsora* spp. on five *Salix* genotypes in monocultures and mixtures in regular and random spatial arrangements	Genetic richness and spatial heterogeneity	Mixtures showed less damage by rust and beetles than monocultures; no significant effect of structural design was detected, but the trend was for decreased damage in random configurations	Peacock *et al.* (2001), Hunter *et al.* (2002)
Microcosms experiments using litter of nine phenotypes of *Quercus laevis* in monocultures and in mixtures	Intraspecific phenotypic richness and composition	C and N fluxes within single phenotype treatments were significantly, but unpredictably, different from those of mixtures No effect of phenotype identity on soil bacterial or microarthropod communities	Madritch and Hunter (2002), Madritch and Hunter (2005)
Literature review of European forests (especially N Europe)	Species richness and/or composition	Different species and functional types differed in wind resistance; mixtures were not more stable than monospecific stands against windstorms	Dhôte (2005)
Literature review of decomposition rate of single-species litter vs. litter mixtures of several N Hemisphere tree species	Species richness and composition	Sometimes faster decomposition in mixtures; in other studies the effect was similar to that predicted from the decay rates of individual species and their relative contribution to the mixture; in two cases lower decay rate in mixtures; different mixtures involving *Pinus* or *Quercus* showed no consistent effect as compared to monocultures	Hättenschwiler *et al.* (2005)
Meta-analysis of 54 studies of insect herbivory on trees, with emphasis on temperate systems	Species richness and composition	Tree species growing in mixed stands overall suffer less damage by specialized herbivore insects than do pure stands; generalist insects showed a highly variable response	Jactel *et al.* (2005)
Heterobasidium annosum (butt rot) in pure vs. mixed stands under different climatic conditions (mostly N Europe)	Species richness	Incidence of *H. annosum* negatively correlated with tree species richness	Korhonen *et al.* (1998), as cited in Pautasso *et al.* (2005)
Cronartium ribicola rust and *Phellinus weirii* root rot in North American forests	Species richness and composition	Disease spread associated with certain host tree species, rather than with tree richness	Pautasso *et al.* (2005)
Literature review of boreal forests	Species richness and/or composition	Mixed stands not more resistant to fire than monospecific stands	Wirth (2005)

(Continues)

Table 11.1 (*continued*)

Ecosystem type and location	Main biodiversity component involved	Findings	Source
Review of 26 experimental studies on the effect of the diversity of trees in boreal forests on the damage by invertebrate and vertebrate herbivores and pathogen species	Tree species richness and composition, landscape heterogeneity	Species-rich stands not consistently less prone to pest outbreaks and disease epidemics than monocultures. Composition appeared to play a greater role than species richness *per se* Susceptibility to inspect pests decreased with increased isolation of stand within a forest mosaic of non-host species	Koricheva *et al.* (2006)
Experimental boreal forests of *Betula pendula*, *Pinus sylvestris*, and *Picea abies* in Sweden and Finland	Species richness and composition	Monocultures of *B. pendula* and mixed stands containing 25% of *B. pendula* and 75% of *P. sylvestris* showed higher defoliation by insects early in the season than *B. pendula* monocultures or 50–50 mixtures of *B. pendula* and *P. sylvestris*. No difference between monocultures and mixtures late in the season	Vehvilaäinen *et al.* (2006)
Experimental plantations of native tropical trees representing a range of relative growth rate (*Cordia alliodora*, *Luehea seemannii*, *Anacardium excelsum*, *Hura crepitans*, *Cedrela odorata* and *Tabebuia rosea*) in monocultures, and 3- and 6-spp. plots, in Central Panama	Species richness, species and functional trait composition	After c. 4 years from establishment, no consistent general effect of species richness was found on either litter production or decomposition. Litter production was significantly affected by tree species richness and identity, with the majority of intermediate-richness mixtures showing higher litter yields than expected based on monoculture. Litter decomposition also varied with species identity and functional attributes. High-richness mixtures decomposed at rates that were no different from expected on the basis of their component species. However, individual species changed their decomposition pattern depending on the richness of the litter mixture	Scherer-Lorenzen *et al.* (2007a)
Experimental decomposition of monocultures and mixtures of 2, 3, 4, and 5 dominant species of central Argentina mountain woodlands, representing a range of functional groups decomposition rates (*Acacia caven*, *Lithraea molleoides*, *Bidens pilosa*, *Hyptis mutabilis*, and *Stipa eriostachya*)	Species richness, species and functional trait composition	When up to five species were included, both species richness and functional composition showed non-additive, mostly positive effects on litter mixture decomposition. The synergistic effects of species richness were significant when the richness of the mixtures changed from 2 to 3–4 species. A greater positive effect was found in mixtures with higher mean nitrogen content and a higher heterogeneity in non-labile compounds. Litter mean quality and chemical heterogeneity were the most important factors explaining decomposability of mixtures	Pérez Harguindeguy *et al.* (2008)

11.3 Making the most of biodiversity in the design of climate change mitigation initiatives

The major hypotheses examined above, and the evidence available so far, indicate that the incorporation of biodiversity considerations has the potential to influence the magnitude and long-term persistence of C-sequestration initiatives. The leading role of the functional traits of locally dominant plant species is supported by strong evidence from a variety of ecosystems. However, considerably more experimental, observational, and modelling work is needed to elucidate many specific details, such as to what extent increasing the small-scale species richness of reforestation or afforestation actions can increase their ability to store C. Nevertheless, we believe that some practical recommendations can already be made based on the current level of knowledge.

• ***Protecting primary forests is the best C sequestration option.*** For obvious practical reasons, to date there is no published biodiversity experiment involving formal experimental manipulation of tree species richness beyond six species. However, primary forests usually have a larger number of species and a wider range of plant functional attributes than do planted forests. They also tend to be dominated by large-sized, slow-growing species that are conservative with resources. Therefore, under both the niche complementarity and mass ratio hypotheses, we expect them to maximize C stocks. Available evidence from the biodiversity and biogeochemistry literature supports this idea. Primary forest ecosystems represent the most important biological C sinks on the planet in terms of both quantity and likely stability through time (Buchmann and Schulze 1999, Valentini *et al.* 2000, Schimel *et al.* 2001, Schulze 2005, Luyssaert *et al.* 2008). With very few exceptions, they contain larger C stocks than younger forests in all biomes (Pregitzer and Euskirchen 2004, Schulze 2005). Recent studies suggest that C outputs and inputs in primary forests are frequently not at equilibrium, and that such forests are active, albeit sometimes small, C sinks (Schimel *et al.* 2001, Schulze *et al.* 2002, Sabine *et al.* 2004, Schulze 2005, Luyssaert *et al.* 2008). In temperate and boreal zones, forests contain large quantities of carbon and can continue accumulating it for centuries (Luyssaert *et al.* 2008). There is less empirical information for tropical forests, but their C exchange appears to be approximately balanced, or even slightly positive (Schimel 2007, Stephens *et al.* 2007). This points to a gross sink that compensates for emissions due to tropical deforestation and fires. Primary forests often show a lower uptake of C per unit time than do newly established plantations (Gower 2003) but on the other hand they sequester it for a longer time. Also, the process of land conversion, for example during the establishment of a new plantation, often releases very large amounts of C from the soil to the atmosphere (Valentini *et al.* 2000, Guo and Gifford 2002, Pregitzer and Euskirchen 2004). As a consequence, the net balance of C sequestered per hectare is usually more strongly positive in the case of primary forests than for new plantations, with the benefits from the latter being more transitory and uncertain (Schulze 2005). Primary forests are being destroyed at accelerated rates, especially in the African and Latin American tropics (Lambin *et al.* 2003, Fearnside and Barbosa 2004, Shvidenko *et al.* 2005). The amount of forested area lost is still impossible to match by plantation initiatives, and this is likely to continue to be the case for the next several decades. Plantations can also involve high monetary and environmental costs. For example, the monetary cost of sequestering 1 Mg of C by forestation and agroforestry activities has been estimated as being more than triple than that of sequestering the same amount by conservation of already existing forests (van Kooten *et al.* 2004). Another recent study shows that monospecific plantations of fast-growing trees in southern South America have strong negative impacts on water supply and soil fertility (Jackson *et al.* 2005). An additional reason to protect primary forests is that changes in the functional attributes of vegetation over large areas can affect climate directly through water and energy exchange (Chapin *et al.* 2008).

• ***The maximization of short-term C sink strength is unlikely to be the best option for C sequestration in the longer term.*** As explained in previous sections and illustrated in Fig. 11.2, the well-supported mass ratio hypothesis predicts that there is fairly a universal tradeoff between a suite of plant attributes that promotes fast C and mineral nutrient acquisition and loss ('acquisitive' syndrome), and another that promotes slower acquisition but long retention of resources within well-protected tissues ('conservative' syndrome). This suggests that a management regime that simultaneously maximizes rapid C uptake from the atmosphere and its long-term sequestration is unlikely to be found. This is directly relevant to C sequestration initiatives, since at any time a C-sequestering project is launched, a decision should be made in favor of one or the other side of the tradeoff (Aerts 1995, Caspersen and Pacala 2001, Noss 2001). For example, early-successional, light-demanding, fast-growing species should be selected when the goal is to maximize short-term productivity. However, C sequestration in the longer term will be greater in areas dominated by later-successional species that are slower growing but have denser timber, and whose litter decomposes more slowly. In view of this, high sink capacity in the short term should not be considered as the major criterion in reforestation/afforestation initiatives. In general, careful consideration of the species and genotypes chosen for each C sequestration project is needed (Lal 2004). There are strong ecological bases to suggest that fast-growing, genetically homogenous, easy-to-manage, widespread forestry species and genotypes (e.g. members of *Eucalyptus*, *Pinus*, and *Acacia* widely planted in South America, Africa, and East Asia) may not represent the most effective option in terms of long-term C sequestration. Also, the choice of species and genotypes with the appropriate attributes for local (present and projected) climatic and disturbance conditions (e.g. fire proneness, storm, or frost frequency) is very important. The same considerations apply to plantations that serve as sources of solid biofuel, although permanence is obviously less of an issue in that case.

• *Mixed forestry systems might be more stable in the face of environmental variability and directional change than monocultures, and they might sequester C more securely in the long term*. This recommendation is consistent with the niche complementarity hypotheses, as well as the results of several experiments in herbaceous communities. The evidence from forest ecosystems is still inconclusive, and long-term field-scale experimental, observational and theoretical studies are needed to rigorously test whether, how generally, and for how long increasing the number of genotypes, species and functional types can benefit afforestation, reforestation, agroforestry, secondary forest recovery and solid biofuel plantation initiatives. However, thousands of years of agricultural experience point to the use of polycultures as a promising precaution to buffer forest production throughout the year and also against environmental change and variability and pest and weed damage. Tree monocultures often, but not always, promote less SOC accumulation than primary or secondary forests (see Lal 2005, Jandl *et al.* 2007 for reviews). But even in cases where the amount of C sequestered by a monoculture is higher, the use of mixtures of more than one tree species may be a good alternative for small or medium-sized farms, especially in tropical and subtropical areas. This is because mixed plantations provide a wider range of products and opportunities. For instance, fast-growing and slow-growing species provide revenues in the short and long term, respectively; different species provide non-forest products such as fruit at different times of the year and thus improve food security and buffer market risks (Piotto *et al.* 2004, Montagnini *et al.* 2005). These ancillary benefits of mixed plantations and agroforestry systems increase the interest of local stakeholders in establishing and protecting forests and diminish incentives for changing to other land uses (Liebman and Staver 2001, Pretty and Ball 2001, Schroth *et al.* 2002, Piotto *et al.* 2004, Montagnini *et al.* 2005). Sometimes the recovery of the natural forest is limited by animal dispersal of propagules, soil moisture, and competition from herbaceous plants. Mixed plantations offer an alternative in these cases. For example, in Costa Rica, more individuals and species of native trees were found to regenerate in the understorey of mixed plantations than those under monocultures (Guariguata *et al.* 1995, Powers *et al.* 1997, Carnevale and Montagnini 2002).

• *Plantations established with the specific purpose of C sequestration or biofuel production can, and should, be compatible with biodiversity conservation*. It is vitally important that projects supported through the CDMs or other initiatives aimed at increasing C uptake do not come at the direct or indirect cost of clearing natural ecosystems, and that they maintain a high ecosystem-service value from the point of view of local communities rather than simply meeting the C credit priorities of external investors

(Niesten *et al.* 2002, Prance 2002, Fearnside 2006a). Niesten *et al.* (2002), Schulze *et al.* (2003) and Chadzon (2008) provide examples of forestry projects that, rather than decreasing pressure on natural ecosystems, may contribute to their destruction, in the name of the creation of C sinks. Agroforestry practices have the potential to store large amounts of C while at the same time protecting biodiversity. For example, Brandle *et al.* (1992) and Noss (2001) highlighted the potential of planted shelterbelts and riparian forests that store C and at the same time provide wildlife habitat and permanent regional vegetation connectivity. Modeling efforts by Bolker et al. (1995) and Pacala and Deutschman (1995) suggest that species-rich and spatially heterogeneous forests could have a C sequestration potential of up to 50 per cent more than monospecific, spatially homogeneous forests. As in the case of managed forests not specifically designed for C sequestration processes, high inter- and intraspecific genotypic richness, the inclusion of local genotypes, and the maintenance of a rich and heterogeneous landscape increases the value of plantations for local societies, and thus their willingness to protect them. This enhances their potential to preserve their long-term survival and C sequestration capacity (Prance 2002, Díaz *et al.* 2005). On the other hand, local communities have little to win and much to lose (e.g. traditional medicine, cultural and spiritual values, employment) from reliance on monospecific stands of fast-growing (and often introduced) tree species and varieties. The incorporation of what is 'valuable biodiversity' from the local community's point of view is essential for striking the right balance between biodiversity and C sequestration and for ensuring the long-term protection of C-sequestering plantations (Díaz and Cáceres 2000, Prance 2002, Saunders *et al.* 2002, Díaz *et al.* 2005, Canadell and Raupach 2008).

• *Decisions about the species and genotype richness and composition of protected or newly established plantations or agroforestry systems should be tailored to the local context*. It is important to keep an open perspective and to avoid mechanical application of general principles to individual projects without careful consideration of the resource base, prevailing disturbance conditions, scale of the project, and attributes of the organisms (including not only the planted species) and ecosystems involved. A practical way to increase our understanding of how, where, and why different biodiversity components affect the C-sequestration capacity of different ecosystems would be to incorporate an experimental component to climate change mitigation and agroforestry and forest rehabilitation initiatives (e.g. Ewel 1986, Montagnini et al. 2005, Scherer-Lorenzen *et al.* 2005b). Moreover, we are aware of a wealth of information being produced by the forestry sector, but this is not often reflected in the peer-reviewed literature. In this sense, the recent book edited by Scherer-Lorenzen *et al.* (2005a) has made a valuable contribution through making available a large body of difficult-to-access and diffuse literature from the forestry sector. A similar effort with specific focus on key regions (e.g. Latin America, Africa, Southeast Asia) including the wealth of information accumulated by governmental and non-governmental grassroots initiatives, would be valuable for helping find the best options for simultaneous C sequestration and biodiversity protection in primary, managed and planted forests.

11.4 Final remarks

In the past few years, the focus of international mitigation efforts seems to have shifted from cutting fossil fuel emissions to enhancing C sequestration, with the remarkable exception of some actions taken during the most recent COPs (see Introduction). The potential contribution of C sinks to climate change mitigation is clearly less important in terms of C released to the atmosphere, than that of decreasing emissions from fossil fuel burning (IGBP 1998, Prentice *et al.* 2001). Therefore, by no means do we believe that mitigation initiatives are a substitute for cutting fossil fuel emissions, however beneficial for the conservation of biodiversity they would be. That said, there is considerable potential for increasing the world's C stocks through management practices (Watson *et al.* 2000, Niles *et al.* 2002, Fischlin *et al.* 2007, Canadell and Raupach 2008). Considering the dramatic observed and projected consequences of climate change (IPCC 2007), we must exploit this potential to the largest possible extent. Equally important is making sure that C sequestration measures do not backfire in the long term, for instance by ensuring that their overall environmental costs do not offset their benefits.

On the basis of the findings summarized above, and in accordance with other authors (IGBP 1998, Schulze *et al.* 2002, Schulze *et al.* 2003, Fearnside 2006b, Luyssaert *et al.* 2008), we suggest that the conservation of natural ecosystems is the best C sequestration option available. Natural ecosystems, with their ability to simultaneously maintain C stocks, biodiversity, and ecosystem services, and their built-in capacity to cope with environmental change and variability, are the ultimate 'win-win' climate mitigation option. There is no substitute for the C-sequestration capacity of natural forests, nor any practical way to reproduce the biodiversity of some of them (Myers *et al.* 2000) or to substitute for the ecosystem services they provide (Millennium Ecosystem Assessment 2003, Shvidenko *et al.* 2005). There is evidence suggesting that their functional composition is changing and that they are losing species at an alarming rate due to land use change (e.g. Sala *et al.* 2000, Brook *et al.* 2003, Gaston *et al.* 2003), and climate change (Parmesan and Yohe 2003, Root *et al.* 2003, Lenoir *et al.* 2008). In view of this, probably the best long-term C sequestration option would be to encourage scientific and policy efforts that preserve their integrity.

In those areas where afforestation and deforestation will not come at the cost of destroying natural ecosystems (e.g. in degraded, not recently deforested areas, or areas where the forest is unlikely to recover naturally, Appanah and Weinland 1992, Montagnini *et al.* 2005), our findings strongly suggest that built-in biodiversity considerations will not only increase their overall ecosystem-service value (Millennium Ecosystem Assessment 2003), but also specifically enhance their long-term C sequestering capacity. In order to make a difference for mitigating the effects of global warming, the size, longevity, and reliability of biological C stocks are more important considerations than sink rates. Consequently, preserving the integrity of natural systems, and building diverse systems with a careful consideration of the most suitable dominant and subdominant species and genotypes, is probably the most appropriate way forward. This is not free of technical difficulties, but its long-term cost–benefit ratio appears low when all economic, social, and environmental factors are considered.

In view of this, the lack of biodiversity considerations in the main body of the Kyoto Protocol is unfortunate to say the least. Particularly worrying is the fact that in the first commitment period of the CDMs only afforestation and reforestation are included, considering that more than half of the world's forested area is located in developing countries and that they are facing accelerating deforestation rates (Lambin *et al.* 2003, Shvidenko *et al.* 2005). In our view, in order to reverse this trend, biodiversity considerations should be incorporated into C sequestration initiatives. In this sense, the request of some developing countries to incorporate the protection of tropical forests into the second commitment period of the Kyoto Protocol (http://unfccc.int/resource/docs/2005/cop11/eng/misc01.pdf), and the new international interest in avoided deforestation with explicit mention to biodiversity (e.g. REDD) are signs that the tide might be turning towards a more positive direction.

Acknowledgements

This chapter greatly benefited from input by D. E. Bunker, O. Canziani, and N. Pérez-Harguindeguy, and from critical review by M. Loreau. It is a product of Núcleo DiverSus (endorsed by DIVERSITAS and the Global Land Project). It has also benefited from fruitful interactions between its authors and the participants in the DIVERSITAS ECOServices Meeting 'Biodiversity and Carbon Sequestration' (7–10 September 2005, Danum Valley Field Centre, Sabbah). SD was supported by FONCyT, CONICET, Universidad Nacional de Córdoba (Argentina), the J. S. Guggenheim Memorial Foundation and the Inter-American Institute for Global Change Research (CRN II 2015, supported by the US National Science Foundation Grant GEO-0452325) while carrying out research leading to this chapter.

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Preface

This volume serves as an introduction, reference, and survey both of the profound transformation experienced in the last decade by ecology's fast-growing field of biodiversity and ecosystem functioning and of the economics of ecosystem services. Motivated in the early 1990s by environmental concerns over worldwide declines in biodiversity, the biodiversity and ecosystem functioning research area originated as a synthesis of the relatively disparate fields of community and ecosystem ecology. Neither discipline by itself could adequately describe the wide array of possible ecological consequences of biodiversity loss (Loreau *et al.* 2001, Naeem *et al.* 2002, Hooper *et al.* 2005). The first generation of research on biodiversity and ecosystem functioning rapidly grew into a discipline that can be characterized by several features (Loreau *et al.* 2002). First, species or functional group richness was the primary way of operationally defining and manipulating biodiversity. Second, many studies often worked within a single trophic level (usually plants), though microcosm and mesocosm studies using microbes and invertebrates proved exceptions. Third, research efforts considered only biogeochemical processes, especially primary productivity, as ecosystem functions. Fourth, the prevailing mechanisms were limited to niche complementarity (i.e. niche differences lead to greater exploitation of available resources that lead to greater levels of ecosystem functioning) and selection effects (i.e. higher diversity communities invariably contain one or a few dominant species with disproportionate influences over ecosystem function) that were often viewed as opposing hypotheses vying for supremacy. Fifth, local extinction or biodiversity loss was largely considered a random process and experiments focused on producing as many randomly constructed species combinations as possible to explore how biodiversity loss influenced ecosystem functioning. Sixth, the research was largely experimental, complex, abstract, and confirmatory in nature (i.e. simply confirming that changes in biodiversity did indeed change ecosystem functioning). Finally, work on biodiversity and ecosystem functioning was colored by a tremendous debate over interpretation of its findings.

Over the last few years, however, biodiversity and ecosystem functioning research has evolved dramatically. This volume provides a thorough review of the new face presented by the second generation of biodiversity and ecosystem functioning research. Its 21 chapters are written by more than 60 authors who have been at the forefront of this transition. Virtually everything that characterized the first generation of biodiversity and ecosystem functioning research has changed. First, rather than species or functional group richness, the new focus is on trait-based, functional biodiversity, as well as on community composition. Second, biodiversity and ecosystem functioning studies are increasingly multi-trophic and span both terrestrial and marine ecosystems in comparison to the dominance of terrestrial plant studies that typified earlier biodiversity and ecosystem functioning work. Third, trait-based mechanisms of ecosystem functioning have become a major thrust for contemporary biodiversity and ecosystem functioning research, while niche complementarity and selection effects are considered to be co-occurring (not conflicting) mechanisms. Fourth, rather than assuming random local extinctions, much new work on biodiversity and ecosystem functioning employs trait-based extinction probabilities or increasingly uses empirical extinction scenarios to establish its biodiversity gradients. Fifth, compared to the more abstract deliberations of the first generation of biodiversity and ecosystem functioning research, there is now much more attention to the role of biodiversity and ecosystem functioning in restoration ecology, agriculture, invasions, disease, pollination, climate change, and other ecosystem-service-related environmental issues. Finally, consensus has been achieved (Loreau *et al.* 2001, Hooper *et al.* 2005) and the debate that once clouded the interpretation of biodiversity and ecosystem functioning findings has largely abated.

There are also entirely new features of the second generation of biodiversity and ecosystem functioning research as well. Enough studies have now accumulated to allow meta-analyses, which obviate the sometimes subjective interpretation of trends in biodiversity and ecosystem functioning experiments expressed during the earlier contentious period. Second, *in silico*, trait-based simulation modeling of biodiversity and ecosystem functioning relationships at larger scales has augmented the complex and costly combinatorial experimental approach and represents an entirely new and promising method for large-scale biodiversity and ecosystem functioning research. Third, metacommunity theory applied to biodiversity and ecosystem functioning provides additional understanding of ecosystem complexity and stability.

Beyond the basic science of biodiversity and ecosystem functioning, this volume also explores the current state of the economics of biodiversity and ecosystem services. With antecedents in both natural resource and ecological economics, this field of economics incorporates insights from ecology to build an understanding of the ways in which biodiversity and ecosystem functioning contribute to human wellbeing. The field received a major stimulus from the Millennium Ecosystem Assessment's (2005b) focus on ecosystem services – the benefits that people derive from the processes and functioning of both 'natural' and 'managed' ecosystems. By conceptualizing ecosystem processes and functioning as factors in the production of ecosystem services that directly or indirectly benefit people, the Millennium Ecosystem Assessment has brought many ecological questions within the realm of economics. For example, it has made it natural to analyze the trade-offs (in terms of ecosystem services) of alternative ecological configurations. At the same time it has compelled economists to pay serious attention to the ecological stocks and flows that underpin the production of many ecosystem services. This volume explains and expands upon the ways in which the new face of biodiversity and ecosystem functioning research is interfacing with research into the decisions that people make about how to use the resources of the environment.

The contents of this volume

In 2000, the National Science Foundation (NSF) funded a Research Coordinating Network (RCN) entitled 'Biotic Mechanisms of Ecosystem Regulation in the Global Environment' (BioMERGE) to foster collaboration and usher biodiversity and ecosystem functioning research through its maturation phase (Naeem *et al.* 2007). The relationship between biodiversity and ecosystem functioning is also the central theme of the ecoSERVICES core project of DIVERSITAS (http://www.diversitas-international.org/), an international programme that promotes biodiversity science and aims to bridge the science and policy interface. This volume is the final product of a five-year collaboration between BioMERGE and DIVERSITAS.

The volume is divided into four sections. The first section, *Introduction, Background, and Meta-Analyses*, provides the background for the volume. The editors provide the background, historical context, and an overview of the volume's content in Chapter 1, followed by a meta-analysis by Schmid *et al*. (Chapter 2) that quantitatively tests several biodiversity and ecosystem functioning hypotheses using the enormous body of published experimental studies. The last chapter in this section is an historical and quantitative analysis of the impact of biodiversity and ecosystem functioning research by Solan *et al*. (Chapter 3) that quantitatively tests several biodiversity and ecosystem functioning hypotheses using the enormous body of published experimental studies.

The second section, *Natural Science Foundations*, consists of seven chapters. In Chapter 4, Petchey *et al.* describe one of the major contributions of biodiversity and ecosystem functioning research to ecology: an increasing emphasis on functional diversity. Petchey *et al.* illustrate both the advantages and challenges of focusing on functional diversity by reviewing how authors have attempted to quantify functional diversity. Duffy *et al.* (Chapter 5), consider how functional diversity has transformed biodiversity and ecosystem functioning research from a largely confirmatory science to one that is increasingly predictive.

The remaining chapters of the second section address universal challenges for all of ecology, in the context of biodiversity and ecosystem functioning. These are stability and complexity (Chapter 6 by Griffin *et al.*), identifying the mechanisms generating ecological relationships (Chapter 7 by Hector *et al.*), the importance of trophic structure (Chapter 8 by Cardinale *et al.*), microbial ecology (Chapter 9 by Bell *et al.*), and the importance of the spatial dimension and metacommunities in determining the effects of diversity on ecosystem functioning (Chapter 10 by Gonzalez *et al.*).

The third section takes research on biodiversity and ecosystem functioning further than it has ever gone into the human dimension. The first six chapters cover the most pressing environmental challenges humanity faces. Notably, these chapters also highlight a new emphasis on ecosystem services that go beyond the historic focus on primary productivity. Díaz *et al.* consider the effects of biodiversity on the carbon cycle (Chapter 11) as a way to shed light on anthropogenic climate change that has been largely devoid of considerations of biodiversity. Wright *et al.* consider the role that diversity may play in fostering the restoration of degraded or abandoned habitats (Chapter 12). Jackson *et al.* (Chapter 13) consider the importance of biodiversity in the agricultural ecosystems that now cover one third of Earth's terrestrial surfaces, and focus on biological control as a case study. Klein *et al.* (Chapter 14) discuss the critical ecosystem service of pollination, which is equally important for many crops as well as unmanaged or restored systems. The mitigation of disease (Chapter 15 by Ostfeld *et al.*) and biological invasions (Chapter 16 by Engelhardt *et al.*) are two other biotic ecosystem services that are strongly influenced by biodiversity.

What truly makes this volume unique are the chapters of Section 3, which consider the economic perspective. Perrings *et al.* (Chapter 17) provide a synthesis of the economics of ecosystem services and biodiversity, and the options open to policy-makers to address the failure of markets to account for the loss of ecosystem services. Barbier *et al.* (Chapter 18) examine the challenges of valuing ecosystem services and, hence, to understanding the human consequences of decisions that neglect these services. Brock *et al.* (Chapter 19) examine the ways in which economists are currently incorporating biodiversity and ecosystem functioning research into decision models for the conservation and management of biodiversity.

The fourth and final section consists of two chapters, one describing the new, ambitious direction of biodiversity and ecosystem functioning research to become a global science (Chapter 20) and a synthesis of this volume (Chapter 21) by the editors that describes the nature of the progress made thus far and the future directions and challenges that have been covered by the many authors of this volume.

Acknowledgments

This volume is the summation of five years of cooperation among biodiversity and ecosystem functioning researchers and environmental economists fostered through joint meetings between BioMERGE and BESTNet (NSF-funded Research Coordination Networks) and the ecoSERVICES project of DIVERSITAS. This collaboration was founded on the principles of inclusiveness (i.e. including participants irrespective of their position on the issues), attention to balance across the various stages in scientific careers (i.e. include graduate students, postdoctoral researchers, junior and senior faculty), and gender balance.

Justin Wright, the first associate director of BioMERGE, coordinated meetings in Seattle (2002) and the Missouri Botanical Garden (2003). Daniel Bunker, the second associate director of BioMERGE, and Andy Hector, the then co-chair of DIVERSITAS' ecoSERVICES core project, coordinated meetings in Borneo (2005) and Switzerland (2006) with the help of Chris Philipson, Glen Reynolds, Philipppe Saner, and Maja Weilenmann. Two ecoSERVICES workshops in Paris, coordinated by John Tschirhardt (2005) and Charles Perrings (2007), laid the groundwork for the economic chapters included in the volume.

The bulk of the funding for BioMERGE came from NSF grants # 0130289 and 0435178 with additional support from the University of Washington, Seattle, and Columbia University. Funding for BESTNet came from NSF grant # 0639252. DIVERSITAS contributed both financial and logistical support to a number of the preparatory workshops, and in particular supported the participation of non-US participants. This volume and its contents serves as a testament to the value of supporting international cooperation, integration, and synthesis among social and natural scientists in basic and applied research.

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