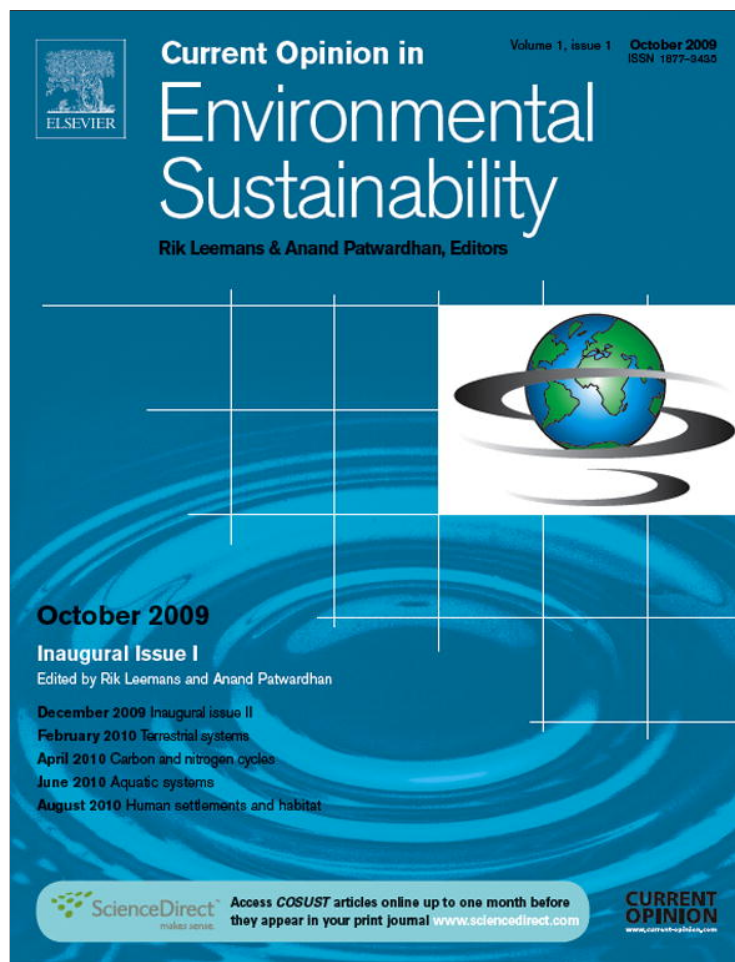


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 Current Opinion in
**Environmental
 Sustainability**

Biodiversity in forest carbon sequestration initiatives: not just a side benefit

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One way of mitigating global climate change is protecting and enhancing biosphere carbon stocks. The success of mitigation initiatives depends on the long-term net balance between carbon gains and losses. The biodiversity of ecological communities, including composition and variability of traits of plants and soil organisms, can alter this balance in several ways. This influence can be direct, through determining the magnitude, turnover rate, and longevity of carbon stocks in soil and vegetation. It can also be indirect through influencing the value and therefore the protection that societies give to ecosystems and their carbon stocks. Biodiversity of forested ecosystems has important consequences for long-term carbon storage, and thus warrants incorporation into the design, implementation, and regulatory framework of mitigation initiatives.

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Current Opinion in Environmental Sustainability 2009, 1:55–60

This review comes from the inaugural issues
 Edited by Rik Leemans and Anand Patwardhan

1877-3435/\$ – see front matter
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DOI 10.1016/j.cosust.2009.08.001

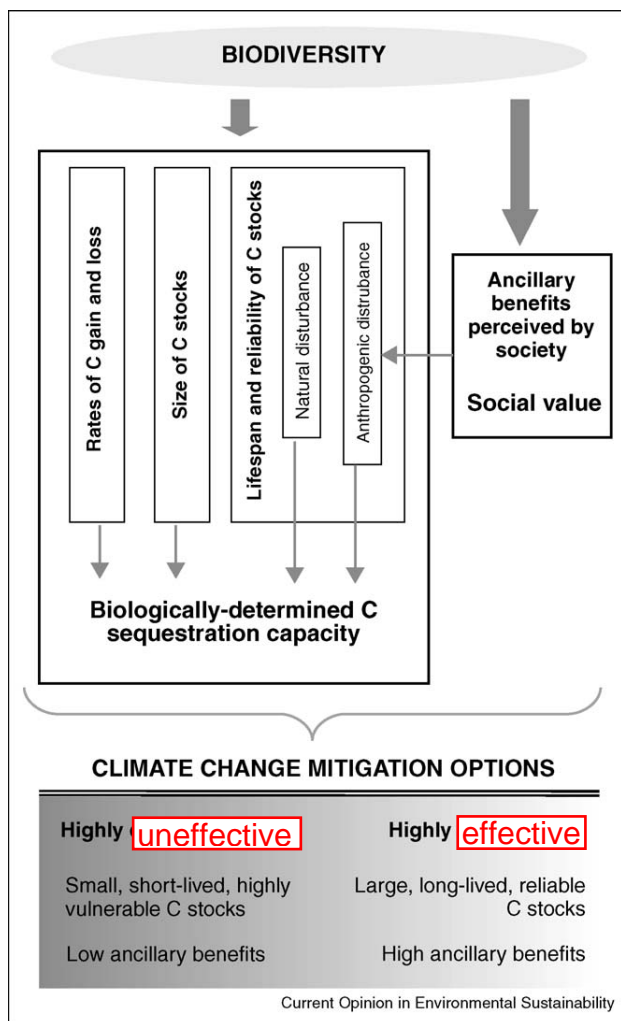
Introduction

Climate change mitigation through the sequestration of carbon and the protection of biodiversity have both been high priorities in the scientific, governmental, and civil-society agendas of the last few years, but they have rarely been considered in conjunction. In international mechanisms aimed at mitigating the ecological impacts of climate change, biodiversity considerations have received only marginal attention, often as ‘ancillary benefits’; that is they are seen as desirable but not instrumental in achieving the main goals. The best example of this is the United Nations’ Kyoto Protocol, intended to slow

down the human contribution to emissions of carbon dioxide and other greenhouse-effect gases to the atmosphere. This mechanism promotes net carbon sequestration in the biosphere as one way to stabilize carbon dioxide and methane levels in the atmosphere. Biodiversity concerns, scarcely present in its original formulation, have gradually been incorporated into the frameworks and guidelines related to the subsequent implementation of the Kyoto Protocol. As such, the Clean Development Mechanism (CDM) and the proposed Reduced Emissions from Deforestation and Forest Degradation (REDD) initiatives, explicitly mention that carbon sequestration activities should be compatible with the preservation of biodiversity. This represents a significant advancement, but biodiversity is still considered as a rather general ‘side benefit’ at best.

In this article, we refer to biodiversity as the number, abundance, composition, spatial distribution, and interactions of genotypes, populations, species, functional types and traits, and landscape units in a given system [1]. Functional traits are physiological, structural, behavioral, or phenological characteristics associated to the response of organisms to the environment and their effects on the functioning of the ecosystems in which they live [2]. We refer to biological carbon sequestration as the maintenance or enhancement of carbon stocks in the biosphere. What really matters for climate regulation by ecosystems is net carbon sequestration, that is, the stability or increase of the vegetation and soil carbon stocks over long periods of time [3,4]. This depends on firstly, how fast carbon is captured and transformed into biomass by plants; secondly, how fast it is lost from the system through animal and microbial respiration (notably through decomposition processes), and other leakages to the air and water bodies; thirdly, how large the stock is when at near equilibrium; and fourthly, how likely the stock is to be released by natural and anthropogenic episodic disturbance or extreme events (Figure 1). In international negotiations and policy instruments, the emphasis has been mostly on the first of these four points, that is, the speed at which carbon can be removed from the atmosphere by plants. Similarly, biodiversity has often been reduced to the number of species present at a site, largely ignoring all other components, such as species and genotype identity, their functional trait composition, relative abundance, and spatial distribution. In our view, this double oversimplification of concepts is one of the causes for the poor articulation between international mechanisms for

Figure 1



How biodiversity influences carbon sequestration initiatives. The effectiveness of climate change mitigation initiatives based on the biological sequestration of carbon (C) depends on two main components: firstly, the biological capacity of the plant–soil system to maintain a positive balance between C gain and loss over time; and secondly, the ancillary benefits provided by the system to societies. The higher these benefits, the more likely societies are to preserve the C stock, thus increasing its long-term persistence. Biodiversity in the broad sense has the potential to alter both components, both positively and negatively. Reliability of C stocks refers to the probability of being affected by natural disturbance (e.g. pest outbreaks, storms, and lightning-initiated fires) or by anthropogenic disturbance, including shifts in land use (modified by permission of Oxford University Press from Ref. [50]).

climate change mitigation on the one hand, and those for biodiversity protection, on the other.

In this article, we focus on forested ecosystems to highlight the fact that biodiversity considerations are not simply a side issue in carbon sequestration initiatives, or something that can come as an additional benefit (or even be sacrificed) in some situations. As such, we

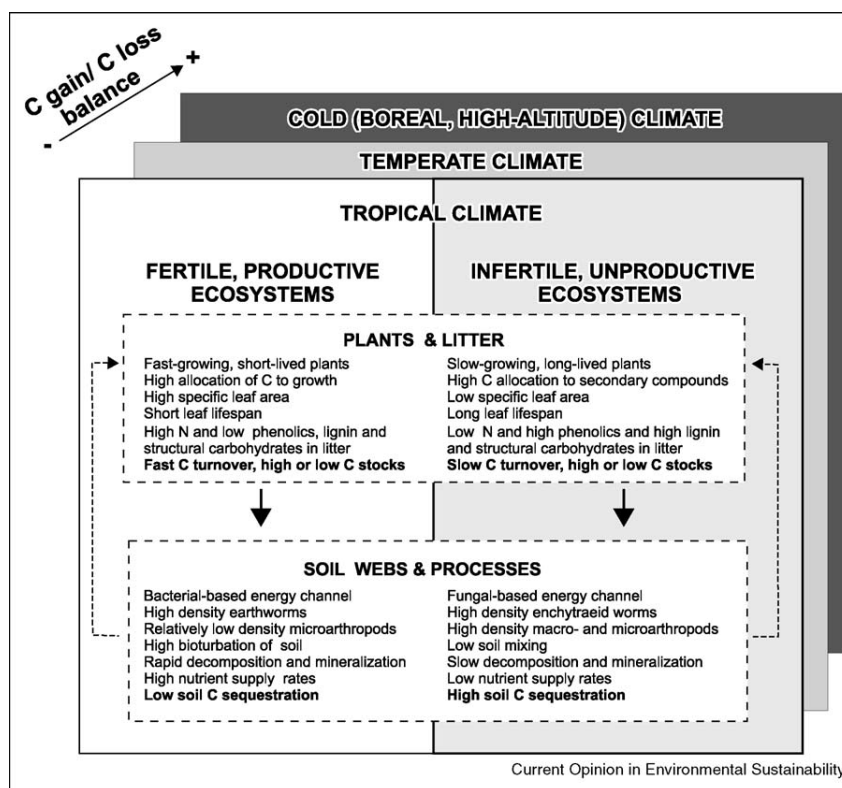
make the case that biodiversity considerations offer an active opportunity to influence the amount, rate, and persistence over time of carbon sequestration in forested ecosystems. Our main focus, therefore is not on how carbon sequestration projects can enhance biodiversity, but rather how the protection and manipulation of biodiversity in the broad sense can enhance carbon sequestration capacity in climate change mitigation projects. By highlighting the multiple ways in which biodiversity can influence forest carbon sequestration, we aim to contribute to the development of more effective, integrated ways of dealing with the dual environmental challenges of carbon sequestration and biodiversity protection.

Direct effects of biodiversity on carbon sequestration

Well established principles of theoretical ecology and empirical evidence from case studies that have accumulated in the past few years, indicate that different components of biodiversity have the potential to modify the turnover rate, magnitude, and long-term permanence of the terrestrial biosphere’s carbon stocks and fluxes. Dominant plant species strongly influence the size and turnover rate of the aboveground carbon stocks [5–7]. They are also a primary determinant of the size and turnover rate of soil carbon stocks, at least in the short to medium term. These dominant species effects are determined by the quantity and quality of resources that they return to the soil, which is in turn driven by their functional traits [8,9^{••}]. Within the envelope of a given climate and substrate [10[•]], these traits influence the rates of carbon gain and carbon loss, as well as the size and longevity of the carbon stocks in equilibrium (Figure 2). In productive and fertile ecosystems, plant production (i.e. carbon input) is greater, but plant litter quality and soil activity (and therefore litter decomposition rates, i.e. carbon loss) are also greater as compared to unproductive ecosystems. The net result is that while productive ecosystems have a greater input of carbon and may sometimes store more carbon aboveground, they often also store much less carbon in the soil, and also less carbon overall [8] (Figure 2). Plant root traits, such as root depth, architecture, chemical outputs, and symbiotic associations, may also be important in determining how dominant plant species affect ecosystem carbon storage [11–13]. These root-trait effects are exerted on both superficial short-lived and deeper long-lived soil carbon stocks, and influence the distribution of carbon stored in the soil profile.

One of the key messages of Figures 1 and 2 is that there are fundamental physiological, evolutionary, and biogeochemical tradeoffs that prevent the simultaneous maximization of the rates of carbon flow, and the size and long-term permanence of carbon stocks. In other words, the three components of the left hand side box in Figure 1 cannot necessarily be optimized at the same time and location. Different carbon sequestration practices advo-

Figure 2



Links between the functional composition of biological communities and carbon sequestration. The functional composition of plant and soil communities influences carbon (C) sequestration through tradeoffs and feedbacks. Plant traits determine the quality and quantity of litter and other inputs to the soil and thus affect key ecological processes in the decomposer subsystem driven by the soil biota. As such, within a given macroclimate, the structural and physiological traits of dominant plants strongly influence C and mineral nutrient cycling and thus potentially C sequestration. Sets of plant and microbial attributes conducive to fast C turnover and small equilibrium soil C stocks (left) and those conducive to low C turnover and accumulation of large equilibrium soil C stocks (right) are often mutually exclusive, and in these cases fast intake (left) and high stocks (right) cannot be achieved at the same time. These interactions and tradeoffs between belowground and aboveground systems feed back (dotted line) to the plant community positively in fertile conditions (left) and negatively in infertile ecosystems (right). Belowground C sequestration (and frequently total 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 (modified by permission of Science Magazine and Oxford University Press from Refs. [8,50]).

cated by CDM and REDD mechanisms illustrate different sides of this tradeoff. An emphasis on fast carbon uptake through the use of fast-growing plant species (as often seen in CDM-related carbon sequestration initiatives) leads to lower long-term carbon sequestration in the ecosystem, as illustrated by the left hand side of Figure 2. On the other hand, old-growth forest ecosystems — on which the major efforts of REDD are focused [14^{**},15,16] — tend to be dominated by large-sized, slow-growing species and large, slow-moving carbon stocks (right hand side of Figure 2). Old-growth forests still represent the second largest terrestrial biological carbon stocks on Earth on a per-hectare basis (after peatlands) [17^{**}], and often act as net sinks for carbon [18^{**},19^{**}]. The functional traits of dominant plants can also affect the extent and probability of carbon release from the biological stocks by disturbances whose fre-

quency is likely to increase in the future as a result of climate change [20]. Traits like canopy height and structure, root depth and architecture, wood structure and leaf morphology and chemistry affect susceptibility to drought [6,21], fire [22,23^{*},24], pest outbreaks [25], and extreme weather events [6,26].

Functional traits of the dominant plants over large areas can also affect water and heat biophysical feedbacks from land to the atmosphere, and thus affect climate directly, irrespective of their effects on carbon sequestration. For example, leaf stomatal conductance and root depth of dominant plants affect ecosystem evapotranspiration; canopy architecture and leaf morphology and lifespan affect albedo, sensible heat, roughness, and the balance between infiltration and runoff [27^{**}]. All these processes feedback onto the atmosphere and have the potential to

influence climate at the local, regional, or larger scales, depending on the size of the vegetation patches [21,27^{••},28,29].

We emphasize that although the functional trait tradeoffs and feedbacks illustrated in Figure 2 are major determinants of carbon sequestration at any given moment, there are other ones that can also be important. For example, observational and experimental studies show that the composition of plant species and genotype mixtures, and in some cases their richness and spatial arrangement, can significantly influence stand-level properties such as the amount of biomass production [30], its stability [31], nutrient use efficiency [32], soil organic matter quantity and quality [33], litter decomposition [34,35], and susceptibility to pest outbreaks [36].

Because empirical evidence for the effects of these different components of biodiversity in the carbon balance of forest ecosystems is scarce and often anecdotal, we still cannot draw definitive conclusions on the relative importance of each of them under different circumstances and for the different factors (i.e. loss, gain, and permanence) that determine the carbon balance. However, the evidence is sufficient to conclude that the identity, the relative abundance, the number, and the spatial arrangement of species are in principle all likely to have an impact on carbon sequestration. Modeling efforts strongly point to the same direction [37].

Indirect effects through social value

Arguably, carbon sequestration represents a particularly extreme example of the tragedy of the commons. It is essential for the good of the whole humankind and at the same time is not the top priority for any stakeholder in particular. Carbon sequestration initiatives often involve the allocation of land, labor, money, and other resources to a benefit which is spread across humanity and whose returns to the local stakeholders that have invested in it are uncertain. Because of this, the long-term viability of carbon sequestration initiatives should substantially increase if stakeholders at the local to national levels perceive some benefits from them. One way is through the provision by the forest of ecosystem services other than carbon sequestration, such water regulation [38], pollination of important plants [39], or the provision of habitat for important animals [40[•]]. The more valued these other services are, and the more immediate and concrete the returns for those who manage and decide over the forest, the more likely these stakeholders will be to protect the ecosystem's integrity, and therefore its carbon sequestration capacity in the long term [40[•],41–43] (Figure 1, right side). Several schemes are already in place to compensate local forest managers for ecosystem services provided to a wider community (e.g. PES initiatives in Costa Rica [44]), providing a fertile ground to evaluate how these concepts work in practice.

Here, biodiversity in the broad sense can play a crucial role. The components of biodiversity on which the social value of forests depends may overlap to different degrees, trade off with, or be largely independent from those that intervene in carbon sequestration capacity. This is stressed by Figure 1, in which these 'ancillary benefits' of biodiversity are listed separately from those that influence the rate, magnitude, and natural persistence of soil and vegetation carbon stocks. For instance, there is often, albeit not automatically, a compromise between plant traits desirable for food and fodder production and those conducive to carbon sequestration [40[•],45[•]]. Provision of habitat for some wild animals and the regulation of water quality and quantity are examples of ancillary ecosystem services that are more readily compatible with carbon sequestration [40[•],46]. On the other hand, forest fragmentation is not desirable from the point of view of carbon sequestration [24], but ecotouristic and amenity value often depend on the existence of a fragmented landscape in which patches of well-developed forest alternate with more open patches in which attractive flowers, fruits, butterflies, and birds tend to concentrate [47,48]. Perhaps one of the most eloquent arguments for the importance of social value in enhancing the long-term persistence of ecosystems is the case of sacred groves. Because of their local religious, medicinal, and cultural significance, these forested areas usually show a high conservation status despite being surrounded by areas of high population density and heavy pressure over natural resources [42].

Carbon sequestration and biodiversity: shifting to a synergistic perspective

There is increasing international recognition that carbon projects should not compromise biodiversity protection [14^{••}]. In this article we have provided another, complementary angle to the question, that is, how biodiversity considerations can enhance the potential of climate change mitigation initiatives based on carbon sequestration.

We need a more detailed understanding of how different components of biodiversity influence carbon sequestration capacity and the likelihood that societies will maintain these stocks in the long term (left and right boxes in Figure 1, respectively). The next generation of studies on the effects of biodiversity on ecosystem services could thus focus on realistic combinations of species or functional types planted or tended by different social groups under different contexts [40[•],49]. In the meantime, and considering the combined challenge of climate change and rapid land use change, enough knowledge is available to provide relevant advice to carbon sequestration projects, regardless of whether or not they are linked to international mechanisms such as CDM and REDD.

First, climate change mitigation depends much more strongly on the amount and permanence of carbon in the biosphere than on the velocity of its capture; and permanence of carbon stored and the speed with which it is captured depend on different components of plant and soil diversity which can cause these two desirable properties to be in opposition. Albeit incomplete, our present understanding of these relationships can help decisions on what species and species combinations are the most suitable for maximizing carbon sequestration, as well as enhancing the compatibility of carbon sequestration with other ecosystem services under different environmental contexts. Second, carbon sequestration initiatives make sense only if there is a good chance of long-term persistence of the carbon stocks being protected or created. In this, social considerations such as how likely stakeholders are to preserve the stocks or shift to other land uses, are as crucial as biogeochemical considerations. Third, we emphasize that simultaneous maximization of multiple ecosystem services is a desirable goal. However, it would be naïve to think that full multifunctionality of carbon initiatives, that is carbon sequestration with nil or minimum sacrifice of other ecosystem services, can always be achieved. Realizing that different aspects of biodiversity can indeed influence carbon sequestration as well as other ecosystem services (as illustrated in the examples in previous sections) provides a powerful tool to decide when and how carbon sequestration can be best combined with other uses, and when a decision has to be made toward one best prevalent use. In summary, a shift is needed from considering biodiversity as an unavoidable prerequisite for carbon sequestration projects toward making the most of biodiversity in the design of climate change mitigation initiatives.

Acknowledgements

This article is a contribution of Núcleo Diversus, endorsed by DIVERSITAS EcoSERVICES and the IGBP Global Land Project. SD was supported by FONCYT, CONICET, Universidad Nacional de Córdoba (Argentina), and the Inter-American Institute for Global Change Research (GRN 2015 II, supported by the US National Science Foundation Grant GEO-0452325) while carrying out research leading to this article.

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