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A safer bet for REDD+: Review of the evidence on the relationship between biodiversity and the resilience of forest carbon stocks

UN-REDD PROGRAMME

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Multiple Benefits Series **10**

The UN-REDD Programme, a collaborative partnership between FAO, UNDP and UNEP, was created in response to, and in support of, the UNFCCC decision on REDD at COP 13 and the Bali Action Plan. The Programme supports countries to develop capacity to reduce emissions from deforestation and forest degradation and to implement a future REDD mechanism in a post-2012 climate regime. It builds on the convening power of its participating UN agencies, their diverse expertise and vast networks, and "delivers as One UN".

The United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) is the biodiversity assessment and policy implementation arm of the United Nations Environment Programme (UNEP), the world's foremost intergovernmental environmental organization. The centre has been in operation since 1989, combining scientific research with practical policy advice.

The United Nations has proclaimed 2010 to be the International Year of Biodiversity. People all over the world are working to safeguard this irreplaceable natural wealth and reduce biodiversity loss. This is vital for current and future human wellbeing. We need to do more. Now is the time to act.

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Executive Summary

Key Findings

Resilience of forest carbon stocks to climate change, in terms of resistance to and recovery from its direct and indirect impacts, is essential for the long-term viability of REDD+.

There is strong evidence that the carbon stocks of **intact** forests are more resilient than those of degraded or fragmented forest, and hence that reducing degradation should be a key REDD+ activity.

There is a small amount of evidence to suggest that whilst management decisions can increase planted forests' resilience to change, **naturally occurring** forests may be more resilient. This evidence lends some additional support to the rationale for a safeguard on the conversion of natural forest, already justified in terms of emissions reduction.

If a forest is natural and intact, is there additional benefit from higher levels of **biodiversity**? There is good evidence that resilience increases with biodiversity for grassland and savanna ecosystems, but only a few relevant observations for forest. Ecological theory would indicate that the pattern will hold true, but targeted research on the role of biodiversity in forest carbon stock resilience would help to identify which forests are most likely to retain their stocks in future.

There is a growing belief that the carbon stocks of intact, naturally occurring, biodiverse forests are likely to be more resilient to climate change than those of planted, less diverse forests (e.g. Fischer *et al.* 2006; Bodin and Wiman 2007). Resilience in this context means that forests can resist and or recover from the negative effects of climate change. Resistance and recovery will differ between forests for various reasons. This review examines the role of biodiversity and related factors in carbon stock resilience.

In their efforts to limit the speed and severity of climate change, Parties to the United Nations Framework Convention on Climate Change (UNFCCC) have proposed to Reduce greenhouse gas Emissions from Deforestation and forest Degradation, 'plus' to undertake additional forest-related activities (hence: REDD-plus, or REDD+), in developing countries. The list of these activities is subject to negotiation, but Parties have agreed to consider the role of 'conservation, sustainable management of forests and enhancement of forest carbon stocks' (Decision 4/CP.15[1]). This last activity is thought to include afforestation, reforestation and forest restoration.

The Copenhagen Accord[2] includes a commitment to limit global mean temperature increases to 2˚C. Even this change is anticipated to affect forest ecosystems through increasing carbon dioxide concentrations, increasing and more variable temperatures, changes to seasonality and moisture availability, and increasing frequency of climatic extremes and associated fire events. The resilience of forest carbon stocks to each of these changes could be key to the long-term success of REDD+.

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[1] FCCC/CP/2009/11/Add.1, Page 11

[2] agreed by a subset of prominent countries at the 15th Conference of Parties to UNFCCC, but only 'noted' by the full set of Parties to the Convention FCCC/CP/2009/11/Add.1, Page 4

Increasing resilience is one way in which biodiversity conservation might benefit REDD+ (it is already clear that, overall, REDD+ can be expected to benefit conservation, although not universally (Miles and Kapos 2008)). Biodiversity is the variability among living organisms including that within species, between species and of ecosystems (UN 1992). Of these aspects, species diversity is most often addressed in the ecological literature. Forests vary in their diversity as a result of historical, random and environmental factors, including the extent of human impact. That is, biodiversity varies amongst intact, naturally occurring forest ecosystems, and is reduced by forest degradation and fragmentation. Planted forests tend to host less biodiversity than naturally occurring forest.

Hence, we set out to explore three related hypotheses on the factors affecting forest resilience:

(i) It is argued that increasing biodiversity is likely to increase the resilience of forest carbon stocks, not least because of 'functional redundancy' (when many species with differing climate tolerances play a similar role; similar species' relative abundance may then change in response to a changing climate, whilst maintaining the carbon storage function). This is the assumption behind the 'diversity-stability' and 'insurance' hypotheses (Yachi and Loreau 1999; Lehman and Tilman 2000).

(ii) It is argued that the carbon stocks of an 'intact' forest are likely to be more resilient to climate change than those of a fragmented or 'degraded' forest. This is based on evidence that forests subject to existing stresses may be less able to withstand additional stresses (Barlow and Peres 2004; Nobre and Borma 2009).

(iii) It is argued that the carbon stocks of a mature 'natural' forest are likely to be more resilient to climate change than a mature planted forest, because the natural system is likely to contain not only a greater species diversity, but also a greater structural and genetic diversity (Mackey *et al.* 2008). The assumption here is that planted forests are managed in such a way that opportunities for colonisation by native species are reduced, and planted using few tree species, in even-aged stands; it is obvious that these distinctions from natural forest are not universal.

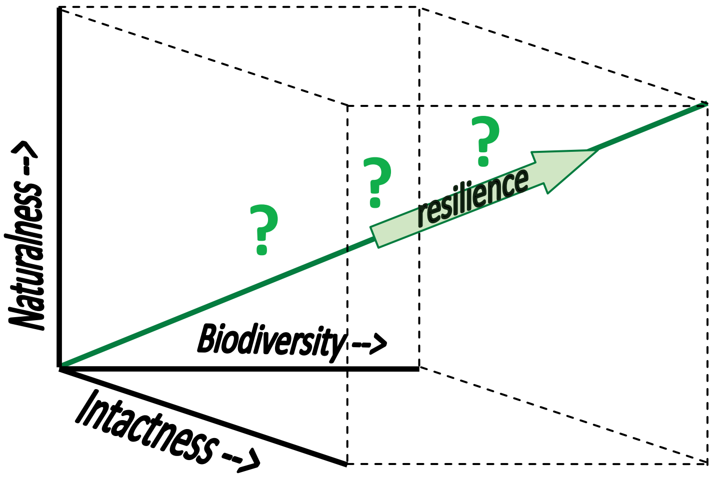

Figure: illustration of the three related hypotheses

Biodiversity, intactness and naturalness all fall along continuous gradients, from low to high, rather than being binary concepts. For simplicity, the Figure above shows a linear relationship between these attributes and resilience of forest carbon stocks; it is likely that the shape of any actual relationships will vary depending upon the forest types and the measures used.

In this paper, we examine the evidence from ecological theory and models, reported observations and experiments that directly address this set of hypotheses. As the set of experimental evidence from forest is small, we also sought out relevant literature on other terrestrial ecosystems. We have not undertaken additional fieldwork or statistical analysis.

Briefly, we conclude that:

(i) There are strong claims in the literature for the role of biodiversity in promoting resilience. While there is also good experimental and theoretical backing for the hypothesis that higher levels of biodiversity will increase the resilience of biomass to climate change, most of this research tackles grassland rather than forest biodiversity. It seems likely that more diverse forest will be more resilient, but much of the hard evidence for this supposition is based on results for other ecosystems.

(ii) There is good evidence that tropical forest intactness will aid resilience of its carbon stocks to climate change. This delivers a strong message that reducing degradation in these forests, caused by anthropogenic fire and destructive logging practices, is key to promoting carbon stock resilience. This has clear implications for national REDD+ strategies: control and monitoring of deforestation alone may be a more risky strategy than if degradation is tackled too.

(iii) There is a small amount of evidence on the comparative resilience of natural and planted forest to climate change impacts (only three papers that met our search criteria). This evidence lends some additional support to the rationale for a safeguard on the conversion of natural forest, already justified in terms of emissions reduction.

There are good reasons to focus REDD+ attention on biodiverse, natural forests, regardless of the evidence on resilience. First, these forests have multiple values in addition to their role in carbon storage and sequestration – such as providing livelihood benefits, biodiversity conservation and vital ecosystem services. Retaining these forests and improving their conservation status will thus contribute to national goals in addition to climate mitigation. Second, in general it is more cost-effective for climate mitigation to prioritise the retention of existing forest above the creation of new forest: per unit area, deforestation involves an immediate and substantial pulse of greenhouse gas emissions, equivalent to the carbon uptake over many years of a newly forested area in the same environment. However, it would be valuable to further investigate the relationship of biodiversity itself to forest carbon stock resilience, devoting more effort to gathering field evidence and undertaking further analyses using existing data.

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1 Introduction

In their efforts to limit the speed and severity of climate change, Parties to the United Nations Framework Convention on Climate Change (UNFCCC) have proposed to reduce greenhouse gas emissions from deforestation and forest degradation, 'plus' to undertake additional forest-related activities (hence: REDD-plus, or REDD+), in developing countries. The list of these activities is subject to negotiation, but Parties have agreed to consider the role of 'conservation, sustainable management of forests and enhancement of forest carbon stocks' (Decision 4/CP.15[3]). This last activity is thought to include afforestation, reforestation and forest restoration. Amongst the 'safeguards' included for discussion in the Ad Hoc Working Group on Long-Term Cooperative Action (AWG-LCA) draft on the topic (FCCC/AWGLCA/2010/14) are proposals that REDD+ activities avoid the conversion of natural forests, and incentivize their protection and conservation.

An improved understanding of this issue should help us to evaluate whether the AWG's draft safeguards on natural forests are necessary for the success of REDD+ itself, or mainly serve to avoid harms to biodiversity and other ecosystem services.

Whilst the original REDD proposal was framed in terms of reducing emissions from changes to natural forest, especially tropical rainforest[4], REDD+ activities could now include maintaining and enhancing forest carbon stocks in planted forest. This broadening of the proposal raises a number of questions, including: what ecosystem services and biodiversity are associated with different natural and planted forests, how much carbon do they sequester, and how stable are those deposits in the face of climate change? The last question forms the topic of this paper.

The ability of forest carbon stocks to resist the pressures of a changing climate, and to recover if they are affected, is critical to their long-term maintenance. Similar considerations apply to the evaporative cooling function of tropical forest (Bonan 2008). This resilience to change is likely to be governed by the physical environment (principally climate and soil), and the type and condition of the forest. If forests are not resilient to the climate change to which we are already committed (even with proposed emissions reductions), their mitigation and adaptation role will be seriously limited.

It is often assumed that intact, natural, forest ecosystems and those with high biodiversity will be more resilient to climate change than degraded, planted and/or less diverse forests. Forest biodiversity conservation is therefore anticipated to be not only an additional benefit of REDD+, but an enabling condition vital to the initiative's success, increasing forest resilience and therefore the long-term stability of carbon stocks.

Forests vary in their biodiversity in response to historical, random and environmental factors, including the extent of human impact. Biodiversity is the variability among living organisms including that within species, between species and of ecosystems (UN 1992). Of these aspects, species diversity is most often

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[3] FCCC/CP/2009/11/Add.1, Page 11

[4] FCCC/CP/2005/Misc.1

addressed in the ecological literature. It varies amongst intact, naturally occurring forest ecosystems, and is reduced by forest degradation and fragmentation. Planted forests tend to host fewer species than naturally occurring forest.

The current paper reviews the published scientific evidence on the role of biodiversity in forests' resilience to climate change. We review what is known about the impact of climate change on forest carbon stocks, assess the evidence on the relationship between biodiversity, intactness and naturalness on resilience, and briefly discuss the implications for policy. A companion briefing (Talbot 2010) assesses the overall state of knowledge on the relationship between forest biodiversity and carbon.

2 Potential climate change impacts on forest carbon stocks

Land-use change has been and will continue to be one of the greatest pressures on forest carbon stocks in developing countries, especially in the tropics. However, climate change impacts are beginning to be felt, and are likely to interact with more direct anthropogenic disturbances, exacerbating the pressures on forests. Temperatures have increased by 0.76°C worldwide in the last 100 years (IPCC 2007a) and there is observational evidence of changes in the distribution of species and composition, structure and function of ecosystems across the world (Parmesan and Yohe 2003; Parmesan 2006; IPCC 2007b; Campbell *et al.* 2009). So far there have been few observed changes in the distribution of forests themselves in response to climate; uphill migration has been observed in some areas (Kullman 2007; Baker and Moseley 2007) whilst in others retreat down-slope followed an increase in drought-related fires (Hemp 2009).

There is clear evidence that climate change will itself have an impact on forests. This could include changes to their capacity to sequester and store carbon and, at worst, the loss of forests themselves. If REDD+ is to contribute to climate change mitigation, we need to know the effects of climate change on forest carbon storage. Our review indicates that forest-based mitigation will only be effective in the context of a broader mitigation strategy to limit the extent of global climate change.

2.1 Potential impacts of change to mean climate

Temperatures are expected to rise globally during the 21st century, with the greatest increases projected for the high latitudes (IPCC 2007c). However, even in tropical regions, forests are likely to experience higher mean, minimum and maximum annual temperatures than at present, and consequently greater moisture stress (though this will vary depending on whether rainfall increases or decreases) (IPCC 2007b; Wright *et al.* 2009). Novel climates with no modern analogue (i.e. unlike any that currently exist on Earth) are more likely to arise in tropical regions (Williams and Jackson 2007). For obvious reasons, it is difficult to predict the responses of species and ecosystems to these climates, though palaeoecological data can offer some clues (e.g. Willis *et al.* 2010).

Our current understanding of how ecophysical processes, such as productivity, are affected by climate change has been gained through modelling and experimental results (Woodward and Lomas 2004; IPCC 2007b; Lloyd and Farquhar 2008; Lloret *et al.* 2009). According to dynamic global vegetation models, over the short to medium term, terrestrial ecosystems could experience a longer growing season, increasing precipitation and carbon dioxide (CO_2) fertilisation benefits, such as enhanced water use efficiency, and should continue to absorb more carbon than they emit (IPCC 2007b). Observational evidence from Amazonian forests suggests that this projection is accurate (Phillips *et al.* 2008).

However, towards the end of the 21st century in a warming world, a reversal is thought likely to occur as these responses reach saturation, and higher temperatures increase both respiration and transpiration (IPCC 2007b; Phillips *et al.* 2008). Modelling work suggests that forest dieback is likely to result under the IPCC's A2 scenarios, mainly due to greater changes in water availability and temperature, especially in tropical, boreal and mountain areas (IPCC 2007b), corroborating the losses of diversity in tropical forests projected by species-based models (Miles *et al.* 2004; McClean *et al.* 2005).

Projected climatic changes are likely to result in a distributional shift in forest biomes. The responses of tropical forests to temperature increases, and hence the implications for forest carbon stocks, are strongly dependent on precipitation changes (Prentice *et al.* 2007). Projected changes in precipitation are more uncertain than for changes in temperature, partly because current global climate models are poor at simulating tropical precipitation, the El Niño-Southern Oscillation and the Madden-Julian Oscillation (IPCC 2007c). Malhi *et al.* (2009) revised the precipitation projections of the IPCC for the Amazon to evaluate the potential impacts of climate change on Amazon rainforests. They concluded that under the A2 scenario, there was a high probability of drier conditions in this region, leading to a shift from rainforest to seasonal forest.

Tropical ecosystems are projected to show an increased turnover of vegetation (i.e. greater mortality and recruitment of individual trees), and a risk of major shifts in forested landscape (forest to non-forest and vice-versa) (IPCC 2007b). Compositional changes are expected, with consequent changes in structure (Campbell *et al.* 2009). These rapid changes may favour species with low biomass density resulting in a decrease of carbon storage and sequestration potential (Phillips 1997; Keeling and Phillips 2007).

Whilst climate may change rapidly, migration rates, which are one limiting factor on species and ecosystem shifts (others include landscape connectivity, soil properties and biotic interactions), may not be sufficient to keep up. Rates of tree migration determined from paleoecological studies suggest that about 100-300m/yr is possible (Pearson 2006; IPCC 2007b). However, projected changes in climate suggest that species would have to move much faster to keep up (Wright *et al.* 2009; Malhi *et al.* 2009). Time lags between climate change and change in species' distributions are evident from other ecosystems (Chapin and Starfield 1997; IPCC 2007b; Devictor *et al.* 2008). This review examines the evidence on resilience to these changes, acknowledging that extreme climate change will tax the ability of any forest to respond.

2.2 Potential impacts from change to frequency of extreme events

Global climate change is also expected to result in more frequent severe weather events, such as drought and storms, which would have significant implications for forest carbon stocks. Drought is projected to become more common in some forest areas, and could lead to reduced ecosystem productivity, changes in carbon fluxes, mortality and reduction in resilience to other disturbances (IPCC 2007b). For example, drought affecting the Amazon during 2005 resulted in a decrease in biomass (Phillips *et al.* 2009). Storms often cause wind-driven tree mortality (Chambers *et al.* 2007; Lindroth *et al.* 2009): a storm in Amazonia in 2005 killed an estimated 320 000 trees in the Manaus region alone (Negrón-Juárez *et al.* 2010). High mortality rates generally lead to a loss of large, old-growth trees and an increase in shorter-lived pioneer trees and lianas (Laurance et al. 2000), which tend to have lower wood density, storing less carbon. This review examines the evidence that biodiversity, intactness or naturalness can increase forests' resistance to and recovery from extreme events.

2.3 Potential impacts from the interaction of environmental change and other stressors

Climate-induced stress, such as drought, may interact with other stressors, such as fire, pest outbreaks and fragmentation, to negate the potential positive effects (mainly increased productivity) of enhanced water use efficiency resulting from moderate increases in CO_2. Indeed, widespread decline in tree growth has been observed across Canadian temperate and boreal forests in recent decades, and this cannot be explained by climate change alone (Silva *et al.* 2010).

Climate change may affect the impact of forest pests through various mechanisms (FAO 2008) and modelling suggests that insect outbreaks may intensify under climate change (Logan *et al.* 2003); though current evidence is inconclusive due to the multiple factors involved (FAO 2008).

Climate change will also increase the frequency of novel (‘invasive’) plant and animal species colonising forest ecosystems, both because the forest area is newly suitable for the invader in climatic terms, and because disturbed ecosystems may be less resistant to immigrating species (Sakai *et al.* 2001). Incoming plant species are more likely than not to increase forest carbon stocks (Liao *et al.* 2008), though depending on the identity and functional role of the invader there will be exceptions.

Forest fires have already shown some evidence of becoming more frequent (Flannigan *et al.* 2000; Aragão and Shimabukuro 2010), and this trend is expected to continue with warming temperatures. Interactions with other disturbances that increase fire vulnerability are likely to negatively affect forest ecosystems and release carbon stocks (Laurance and Williamson 2001; Nitschke and Innes 2006; Bond-Lamberty *et al.* 2007; Nepstad *et al.* 2008). Biodiversity-related factors affecting resistance to and recovery from fire are also covered by this review.

3 What evidence is there that biodiversity, intactness and naturalness affects forest carbon stock resilience?

3.1 Definitions and hypotheses

Resilience of forest carbon stocks to climate change is here defined as both *resistance* to change (also known as inertia), and *recovery* from change (elasticity, or 'equilibrium resilience', sensu Holling and Meffe 1996). A more resilient forest may have a greater ability to retain its biomass carbon under adverse conditions, and/or may recover more rapidly from episodes of loss, than a less resilient forest. There are a wide range of resilience definitions; our approach follows van Ruijven and Berendse (2010). Further definitions may be found in the Glossary (page 25).

We have evaluated the extent to which the peer-reviewed scientific literature supports three broad hypotheses on the resilience of forest biomass carbon to climate change:

(i) That a more biodiverse forest is more resilient to climate change than a less diverse forest
(ii) That an 'intact' forest ecosystem is more resilient to climate change than a degraded or fragmented ecosystem.
(iii) That a mature 'natural' forest is more resilient to climate change than a mature planted forest

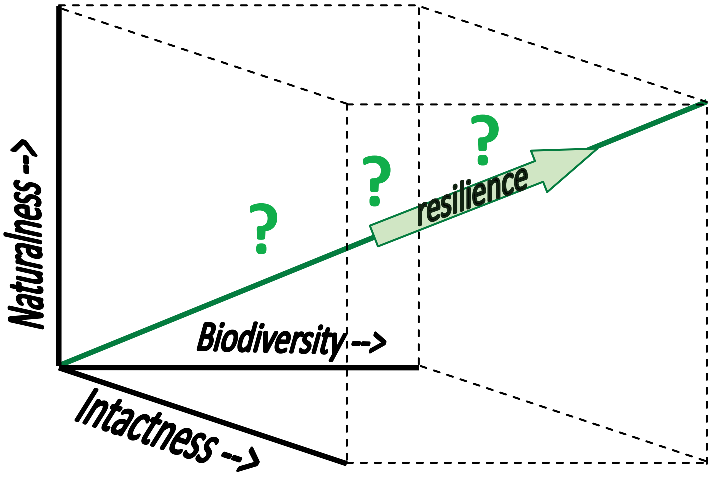

Figure 1: illustration of the three related hypotheses

Each of these attributes of a forest forms a continuous gradient, from low to high, and is not independent of the others.

Biodiversity is the variability among living organisms including that within species, between species and of ecosystems (UN 1992). It can be represented using many different metrics or indicators, depending on the aspect of most interest. Species diversity is most often addressed in the ecological literature. Forests vary in their diversity as a result of historical, random and environmental factors, including the extent of human impact. That is, biodiversity varies amongst intact, naturally occurring forest ecosystems, and is reduced by forest degradation and fragmentation. Planted forests tend to host less biodiversity than naturally occurring forest, and will often be fragmented (isolated in the landscape).

'Intactness' refers both to the status of a patch of forest and the degree of fragmentation of the matrix surrounding it. 'Naturalness' is a continuum representing the extent of (freedom from) human intervention. For simplicity, Figure 1 shows a linear relationship between each of these complex, related concepts and the resilience of forest carbon stocks; it is likely that the shape of any actual relationships will vary depending upon the forest types and the measures used.

The first hypothesis rests on the theory of functional redundancy: when many species with differing tolerances to climate and extreme events are able to play a similar role, their growth rates and relative abundance may change in response to a changing climate whilst the ecosystem remains fairly stable. As well as primary production, these functional roles may include those that plants depend upon, such as seed dispersal (Brodie and Gibbs 2009), and predation of herbivores.

This thinking underpins the 'insurance hypothesis' that high species diversity protects ecosystems from declines in their functioning caused by environmental fluctuations, and the related 'diversity-stability hypothesis', which proposes that productivity is less variable in a more diverse ecosystem (Yachi and Loreau 1999; Lehman and Tilman 2000). If correct, this would imply that variation in resilience to climate change amongst natural forests is at least partially determined by their richness in biodiversity. It would also provide one mechanism for the second and third hypotheses, below, as both the degree of intactness and naturalness affect the status of biodiversity.

The second hypothesis suggests that the carbon stocks of an 'intact' forest are likely to be more resilient to climate change than those of a fragmented or degraded forest. This rests on the assumption that forests subject to existing stresses which reduce or threaten aspects of their biodiversity will be more vulnerable to and less able to withstand additional stresses (Barlow and Peres 2004; Nobre and Borma 2009).

The third hypothesis suggests that the carbon stocks of a mature 'natural' forest ecosystem are likely to be more resilient to climate change than a mature planted forest ecosystem, because the natural system is likely to contain not only a greater species diversity, but also a greater structural and genetic diversity (Hawley *et al.* 2005; Mackey *et al.* 2008; Schaberg *et al.* 2008). The assumption here is that planted forests are managed in such a way that opportunities for colonisation by native species are reduced, and planted using few tree species, in even-aged stands; it is obvious that these distinctions from natural forest are not universal.

There is a related 'diversity-productivity' hypothesis, which proposes that productivity increases with increasing biodiversity. The 'overyielding' effect known from forestry demonstrates that plantations of mixed tree species tend to produce more than when the same species are grown in monoculture (Erskine *et al.* 2006; Potvin and Gotelli 2008; review in Thompson *et al.* 2009). Mechanisms could include complementarity (species with differing requirements can make use of more of the overall resources), facilitation (species grow better side by side for various ecological reasons) and in some circumstances, sampling effects (species-rich plots are more likely to include the more productive species from the available pool). It is less clear whether differences in biodiversity between natural forests occupying similar environmental conditions have significant impacts on productivity (Talbot 2010).

It could be argued that the first hypothesis is supported by this evidence from plantations and experimental ecosystems (e.g. Naeem *et al.* 1994) that biodiversity leads to greater productivity. If loss of diversity leads to loss of productivity, and if this trend accelerates with decreasing biodiversity, the loss of any random species from a less diverse system would be more likely to lead to carbon loss than an equivalent loss from a more diverse system. This argument is clearly stronger when comparing relatively low-diversity forests, as in these communities, loss of functional diversity is more likely to accompany reductions in species diversity. We have not included research on biodiversity-productivity relationships within the current review (see Box 1 below).

3.2 Methods: Distinguishing different types of evidence

We undertook a semi-systematic review of the literature: that is, we searched for relevant peer-reviewed literature using Web of Knowledge and Google Scholar, and also followed up selected citations from within these references, and asked reviewers to suggest any missing examples. These second steps depart from systematic review methodology, but were adopted because the useful literature discovered using searches alone was sparse.

Box 1 lists the criteria used to include or exclude papers. We focused most attention on finding papers pertinent to tropical and subtropical forests, but also sought out relevant papers on other forest types and other terrestrial ecosystems (grassland, wetland etc.), and even experimental microcosms. These other ecosystem types were included because initial discussions and our early searches had indicated that the evidence for tropical forest was likely to be limited.

We classified each paper according to whether it was primarily of interest because it contained evidence from experiments, observations, modelling based on ecological data, or theory, and identified whether it supported or rejected any of the three hypotheses listed above. Here we define experiments as involving manipulation of ecosystems, whilst observations record existing patterns. We propose that experimental evidence is given the most weight, followed by observations, modelling and theory in that order.

Box 1: Criteria for inclusion of papers in the review of the evidence

Only research on terrestrial ecosystems (including experimental ecosystems).

Only papers that present evidence or contributions to theory – no unsubstantiated claims.

Only papers that offer support for or against one of the hypotheses by considering the role of biodiversity/intactness/naturalness in resilience (may be described as permanence, resistance, stability, recovery) to climate-related changes of above-ground biomass or carbon stocks. Not papers focused on relationships with the size of stocks, productivity, sequestration potential: only direct evidence on resilience.

> …including comparisons of resilience in forests with different levels of biodiversity, intactness or naturalness.
>
> …including tests of proposed mechanisms by which biodiversity, intactness or naturalness affect resilience.

No papers considering resilience to largely unrelated factors such as herbivory, or to invasive plant species which may actually increase carbon storage (Liao *et al.* 2008).

No literature reviews (e.g. Noss 2001; Hooper *et al.* 2005; Thompson *et al.* 2009), to ensure that evidence is not double-counted.

Only papers that we were able to access in full within the review timescale!

3.3 Findings

Table 1 summarises the evidence for the three hypotheses arising from studies of tropical forest. Table 2 summarises all the evidence from terrestrial ecosystems, including for tropical forest. Where multiple papers described the same theory or results, we only counted this as one piece of evidence in our summary table. In all, 30 cases (papers or sets of papers) met the criteria for inclusion described above. Eleven of these concerned tropical forest. For brevity, only the evidence from observations and experiments are discussed individually below; all the papers featured in the tables are listed in Annex I.

Biodiversity

Is a more biodiverse forest more resilient to climate change than a less diverse forest?

While there is good experimental and theoretical backing for the hypothesis that higher levels of biodiversity will increase the resilience of terrestrial ecosystems to climate change, the evidence for forest itself is more limited. Grassland is a frequent subject of experimental studies, as it is easier to observe and/or manipulate over shorter timescales than forest. Here we report on four grassland experiments, one from an artificial microbial community, two observations from tropical forest, one from temperate forest, and one observation from Australian savanna.

We identified only two reported observations for tropical forest. In Western Polynesia, less numerous bat species were observed to take up the seed dispersal function from previously more numerous species affected by pressure from cyclones and fire, promoting resilience of the original forest structure (Elmqvist *et al.* 2003). This evidence supports the insurance hypothesis, but lacks a control case. Meanwhile, in Jamaica, hurricane damage was observed to be less serious in the least biodiverse of four montane forests studied (Tanner and Bellingham 2006). It was hypothesized that the low mortality in this forest resulted from its short trees, and soils that allowed greater flexion of stems in the wind, rather than being related to species diversity itself. Hence, our survey identified one case in which resistance to extreme events was higher because of diversity itself, and one in which resistance was lower because of factors correlated with higher diversity. This is far from sufficient to draw conclusions on the overall response of forests to climate change.

In an early experimental study in the Serengeti National Park (Tanzania), the resistance of ungrazed tropical grassland biomass to high variations in rainfall over a five week period was observed to correlate with species diversity, when monitoring adjacent stands (McNaughton 1977). A Shannon-Weaver index was used to measure biodiversity.

In contrast, an eleven-year prairie grassland experiment used differing levels of nitrogen enrichment to influence biodiversity over 207 plots, with more nitrogen leading to less species richness but more biomass (Tilman and Downing 1994; Tilman 1996). Their conclusions that the results support the diversity-stability hypothesis, and that biodiversity increases recovery of biomass to extreme drought, appear to discount the alternative explanation that the findings resulted from variation in the limiting factor for productivity (nitrogen versus water) amongst the different plots (Huston 1997). This explanation argues that the less biodiverse plots with greater nitrogen availability were able to respond positively to additional water, and thus experienced greater interannual variability in productivity, and their greater biomass was less resistant and recovered more slowly from drought. Whilst these experiments also yielded some direct evidence for the insurance hypothesis, with some species increasing as others declined during the drought, its design makes the results difficult to interpret.

The same team devised an alternative experiment using 168 plots on a field purged of its vegetation, seed bank and topsoil, which excluded the effects of nutrient availability. Different mixes of up to 16 grassland species were planted and their biomass monitored over ten years (Tilman *et al.* 2001; Tilman *et al.* 2006). After correcting for the increase in biomass through time as the plots matured, the more diverse plots were more stable through time (that is, more resistant to the effects of interannual variation in climate). Species diversity and functional diversity were also positively associated with productivity, in contrast to the nitrogen-based experiments above. One reason for this productivity pattern is that a higher diversity plot is more likely to include the larger of the species from the sample set (Huston 1997).

In a very similar experiment in the Netherlands, ecologists assessed the response of 102 seven-year old plots to the two-month summer drought of 2006 (van Ruijven and Berendse 2010). Careful analysis indicated that resistance to drought decreased with biomass, and was not directly related to species richness. Nor was the overall resilience, defined as the ratio between post-drought and pre-drought biomass. However, the recovery of biomass (both total or proportional increase after the drought) was predicted by richness, and not by pre-drought biomass (itself correlated with richness). This result depended upon the response of a single grass species, which recovered more successfully in diverse mixtures than in monoculture. These data therefore reject the insurance hypothesis for resistance to a single drought, but support it (and the facilitation mechanism for productivity) for recovery.

Detailed observations on the functional mechanisms by which the insurance hypothesis might function were made in a comparison of lightly and heavily grazed Australian savanna (Liao *et al.* 2008). The relative abundance and functional attributes (estimates of height, mature biomass, specific leaf area, longevity and leaf litter quality) of the grass species present were recorded. It was inferred from the insurance hypothesis that where the most common (dominant) species declined as a result of heavy grazing pressure, one or more functionally similar species would increase in response[5]. Knowledge of the different species' functional attributes made it possible to predict which species would be most likely to respond and multiple to fill the empty niche. Two of three, or three of four species (depending on the precise test) responded as predicted, lending support to the hypothesis.

The insurance hypothesis was also investigated in a set of 318 experimental microcosms with different nutrient and light levels, each initially populated by a known (but varying between microcosms) community of microbes including algae, other protists and bacteria (Naeem and Li 1997). In these closed environments, some species went extinct, either as a result of random factors, or because of low tolerance to the given environmental conditions. The biomass of more diverse communities was more resilient to local extinctions, with other species in the same functional group as the lost species increasing in response.

Finally, genetic diversity-resilience relationships were studied through observation of natural temperate pine forest (*Pinus banksiana*) (Schaberg *et al.* 2008). Repeated lightning-induced fires in the area had created four distinct even-aged stands, from 22 to 68 years old, which came from the same genetic stock. The higher genetic variability (heterozygosity) found in the older populations indicated that natural selection had favoured hybrid vigour. The implication is that individuals low in heterozygosity are more likely to succumb to environmental stresses; thus, that genetic diversity promotes resistance.

How much account should we take of the evidence from grassland, savanna and microbial communities when judging the forest biodiversity-resilience hypothesis? The ecosystems differ in many ways from undisturbed tropical forest: most obviously in their shorter-lived dominant plant species, very small spatial scale, more temperate climate systems, lower total diversity, lower biomass per unit area, and substantial human manipulation to simplify the experimental systems. In favour of extrapolating the results to forest, we note that the authors intend their experiments to test ecological theory on diversity, choosing their model ecosystems for reasons of convenience.

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[5] As there are no 'before and after' measurements for the grazed site, it was necessary to assume that the dominant species would have been the same in both sets of plots without the heavy grazing pressure.

All results do show that biodiversity has positive effects on resilience. If the patterns identified hold true for forest ecosystems, biodiverse ecosystems with a greater number of 'redundant' species (those with a similar function) would show a greater resistance to and recovery of biomass carbon stocks from climate change impacts. Several theoretical papers from grassland or generic communities also support the hypotheses, including one on the role of genetic diversity (Bradshaw 1991). A conservative approach would suggest that whilst direct work on the role of tropical forest biodiversity would be very useful, it is more prudent to assume that the same patterns will hold for forest than to ignore this probable role of biodiversity.

Intactness

Is a more intact forest more resilient to climate change than a more degraded or fragmented forest?

There is good evidence that tropical forest intactness will aid resilience of its carbon stocks to climate change, with three sets of supportive results from experiments reported, and three sets of observations (one rejecting the hypothesis). One supportive case was found for grazed ecosystems, and one study considering the effect of repeated selective logging on forest genetics.

All six tropical forest papers relate to Amazonia, partly because the Biological Dynamics of Forest Fragments Project (BDFFP) has been underway here since 1979. This project created a range of forest patches of different size within intact tropical rain forest, spanning circa 1 000km^2 near Manaus in Brazil. This framework allowed evaluation of the influence both of patch size and distance from edge on tree life history in fragmented forest. The earliest relevant results indicated that the smaller the patches of forest, the lower the resistance to mortality from wind-throw, with significant losses of above-ground biomass (Laurance *et al.* 1997; Laurance 1998). These wind-throw effects resulted from the fragmentation directly, but the results may also be applicable to response to extreme weather events. Later results showed that the resistance of large trees to damaging processes, including drought, reduced with decreasing patch size (Laurance *et al.* 2000). The rate of mortality was high enough that recovery of carbon stocks was thought likely to be affected by diminished recruitment of large tree species.

In the 1997 El Niño Southern Oscillation drought, mortality in the BDFFP region increased, and did so to a greater extent in trees closer to the edges of the fragments (Laurance and Williamson 2001). If this is roughly indicative of the impacts of a warming climate, we can conclude that carbon stocks in intact forests will be more resilient than those in fragmented ones.

Of the observations, two report measurements of fire vulnerability in the eastern Amazon, and the other is a remotely sensed assessment of forest photosynthesis (via a 'greenness' index) over the entire basin. These study are unconnected to BDFFP. The fire research indicates that forest degraded by logging and previous fire is less resistant to later fire episodes than undisturbed forest, with regenerating forest more resilient than recently logged forest. This evidence draws from two field studies, the first using four 40-metre transect established in one area in 1987 (Uhl and Kauffman 1990), and the second considering 10 x 0.5 hectare plots dispersed over 100 km from 1996 to 1997, and using remotely sensed imagery to identify the frequency of fires here (Cochrane *et al.* 1999; Cochrane 2001;

Cochrane and Laurance 2002). Forests within around 2 km edges were predicted to be more vulnerable to fire, and newly burned forests create more fragmentation. Note that when tropical moist forests do burn, they are very flammable: fire and drought have caused significant mortality in central Amazonian forest (Barlow and Peres 2004). Damage can be so severe that only a few trees per hectare remain.

The second study investigated the response of Amazon forest to the 2005 drought, to test the hypothesis that photosynthesis would be affected (Saleska *et al.* 2007). It found that the only observable negative impacts from the drought were in areas heavily affected by human activity, indicating that intact forests have superior resilience. A recent paper disputes these results (Samanta *et al.* 2010), but is in turn hotly disputed by the original authors (Saleska 2010).

In Indonesian Borneo, biomass recovery in forests that had burned in 1998 was compared (Slik *et al.* 2008). One set of forest plots had burned 15 years previously, whilst the others were not known to have burned before. There was no significant difference between the two sets, with both showing little recovery or further decline. At least at these time intervals, fire has little influence on this aspect of resilience to later fire. Taken together with the Amazon results, we may conclude tentatively that existing degradation decreases resistance to fire, but does not decrease the (generally poor) rate of recovery.

Observations from subtropical arid grassland plots over a gradient of disturbance by grazing identified that survival of perennial plants during drought, and recovery from drought, was higher in the less degraded grasslands (Whitford *et al.* 1999). This finding offers further support to the hypothesis.

One final piece of evidence from Amazonia indicates that even intact forests can be vulnerable to climate-related changes. The dominance of large lianas has been increasing, with resulting increases in tree mortality and decreases in growth (Phillips *et al.* 2002). It is probable that this issue would be less of a problem for carbon stocks in a managed plantation. As there is no comparison with degraded forest, these findings are not featured in the Tables.

Naturalness

Is a more natural forest more resilient to climate change than a planted forest?

Very little literature was found that compared the resilience of natural and planted forest to climate change impacts: we have identified only one tropical and one temperate example. In addition, a review of the resilience of low-diversity planted temperate forests to insect pests, disease and fire asserts that well-managed plantations will be more resilient to these pressures than natural forest, especially when non-native tree species are used (Gadgil and Bain 1999). The thinking is that vulnerability of non-native trees to local herbivores and disease will be low, and that an open understorey and careful planting patterns will mitigate against many of these threats. However, this paper is too speculative in its comparisons between natural and planted forest to justify inclusion in the table.

One paper did compare the effects of water stress on planted and natural forest remnants of the same temperate pine species, in the dry steppe of Kazakhstan (Usol'tsev and Vanclay 1995). The biomass of the natural forest was significantly more resistant to recurrent drought conditions, such that plantation die-back was common. Unfortunately the plantations were created on rich humus soils, whilst the natural forest grew on sandy soils, which makes the results difficult to interpret strictly in terms of naturalness. Nonetheless, the conclusions were that the planting density, site preparation and maintenance practices were major factors in the differences between the two forest types, with the natural forests producing much denser stands and deeper roots.

The same Jamaican hurricane discussed in the biodiversity section also had impacts on planted pine (*Pinus caribaea*) forest. Rigorous comparisons between the plantations and natural forest are not available as the authors were most interested in effects on existing plots in natural forest. However, the plantations were observed to be much more vulnerable to Hurricane Gilbert than any other forest (Tanner *et al.* 1991; Bellingham *et al.* 1992). About 80% of pines were broken or uprooted. It is suggested that this vulnerability arises from the even-aged structure of the plantation, and also noted that species adapted to growing in exposed positions tended to be less vulnerable. Whilst this implies that the choice of plantation species would have a strong effect on their resistance to hurricane damage, impacts on natural, coastal *P. caribaea* forests in Nicaragua were much smaller than to inland rainforests exposed to a similar force wind (Boucher *et al.* 1990). This lends tentative support to the idea that the even-aged structure is responsible for the lack of resilience.

Species composition also clearly influences the recovery of forest carbon stocks after wind-throw, with coniferous species regenerating more slowly. The Jamaican natural forests' recovery was observed to be rapid, at least in terms of re-leafing and replacement of broken crowns; there is no equivalent account for the plantation forests, but the Nicaraguan *P. caribaea* showed little resprouting after Hurricane Joan.

Table 1: Evidence reviewed from tropical forests. Superscripts refer to papers in Annex I

Strength of evidence	**Evidence from**	**Hypotheses: resilience is increased by…** (✓ = no. of cases in support of hypothesis, ✗ = no. rejecting hypothesis)						**Total number of cases**
		Biodiversity		Intactness (v degradation, fragmentation)		Naturalness (v planted)		
		✓	✗	✓	✗	✓	✗	
High	Experiments	0	0	3[26 to 30]	0	0	0	**3**
↓	Observations	1[1]	1[23]	3[25, 31 to 33, 35]	1[36]	1[4, 5]	0	**7**
	Modelling	1[10]	0	0	0	0	0	**1**
Low	Theory	0	0	0	0	0	0	**0**
Total		**2**	**1**	**6**	**1**	**1**	**0**	**11**

Table 2: Evidence reviewed from all terrestrial ecosystems, including tropical forest. Superscripts refer to papers in Annex I

Strength of evidence	**Evidence from**	**Hypotheses: resilience is increased by…** (✓ = no. of cases in support of hypothesis, ✗ = no. rejecting hypothesis)						**Total number of cases**
		Biodiversity		Intactness (v degradation, fragmentation)		Naturalness (v planted)		
		✓	✗	✓	✗	✓	✗	
High	Experiments (forest)	0	0	3[26 to 29]	0	0	0	**3**
	Observations (forest)	2[1, 24]	1[23]	3[25, 31 to 33, 35]	1[36]	2[4, 5, 11]	0	**9**
	Experiments (other terrestrial ecosystems)	6[2, 3, 6 to 8, 16]	1[16]	0	0	0	0	**6** (‘16’ appears twice)
	Observations (other terrestrial ecosystems)	1[9]	0	1[34]	0	0	0	**2**
	Modelling (forest)	2[10, 12]	0	0	0	0	0	**2**
	Modelling (generic, or other terrestrial ecosystems)	3[13 to 15]	0	0	0	0	0	**3**
	Theory (forest)	0	0	0	0	0	0	**0**
Low	Theory (generic, or other terrestrial ecosystems)	5[17 to 22]	0	0	0	0	0	**5**
Total		**19**	**2**	**7**	**1**	**2**	**0**	**30** **31**

4 Discussion

Overall, we found many more cases related to biodiversity than naturalness or intactness, but the majority of the experimental and observational data for tropical forest related to intactness. This may relate to the relative ease of obtaining data – it is simpler to distinguish intact from degraded forest, than to separate out the influence of biodiversity *per se* on resilience. The latter task is easier with less complex, rapidly responding ecosystems such as grassland.

Intact forests appear to be more resilient than degraded or fragmented forests against some of the impacts of increased temperatures: i.e. drought, increased fire frequency, possible increased storm frequency. This evidence clearly indicates that reducing degradation in natural forests, caused by anthropogenic fire and destructive logging practices, is key to promoting carbon stock resilience.

As remote sensing efforts have concentrated on the estimation of deforestation (or rather, forest cover change) rather than degradation, new approaches to identifying the extent to which carbon stocks are degraded would be valuable. LIDAR and radar technologies may be able to contribute here, in combination with community forest monitoring and more traditional field data collection. The same techniques would also improve the overall estimation of forest carbon stocks.

Despite the relevance of the question both to the safeguard on converting natural forests and to the selection of approaches to carbon stock enhancement, we have found only a little direct evidence on the resilience of natural forest versus plantations. That which we have found indicates that natural forests may be more resistant to wind-throw, and perhaps to water stress.

Strong claims based on ecological theory are made to support the role of biodiversity in enhancing the resilience of forest carbon stocks, but there is less research for forest *per se*. It would be valuable to further investigate the relationship of biodiversity itself to forest carbon stock resilience, devoting more effort to gathering field evidence and undertaking further analyses using existing data.

Given the long time periods over which processes of tree growth, mortality and recruitment occur, there may be difficulties in gathering new evidence rapidly enough to serve the policy needs of REDD+. One solution is to identify potential analyses from existing long-term ecological datasets such as those of the RAINFOR network (Malhi *et al.* 2006). It would be useful to identify the barriers to applying some of the same techniques that have been used to analyse the role of grassland diversity in resilience.

It is worth noting that we have not sought out papers on the resilience of soil carbon stocks, concentrating here on biomass. There is a known positive relationship between forest age and the accumulation of soil carbon stocks through leaf deposits (Schulze *et al.* 2000). The increased vulnerability of degraded tropical rain forest to fire (Barlow and Peres 2004) is likely to lead to accumulation of forest carbon stocks (black carbon) in some soil-climate combinations, and losses in others (e.g. the prolonged underground fires seen in peat forest (Hooijer *et al.* 2006)).

Finally, there are thresholds beyond which any forest will not continue to sequester or even store carbon: it is difficult to ensure resilience against prolonged water shortage or frequent extreme events.

REDD+ can make an excellent contribution to mitigating climate change, but without other measures to limit the scope of the change, this role will diminish into the future as forests are themselves affected by change.

Lessons for REDD+ policy

As biodiverse, natural forests have multiple values in addition to their role in carbon storage and sequestration – such as providing livelihood benefits, biodiversity conservation and vital ecosystem services - and as it is generally more cost-effective for climate conservation to prioritise the retention of existing forest above the creation of new forest, there are good reasons to focus REDD+ attention on these forests regardless of the evidence on resilience.

However, on the current evidence, there is a stronger argument that reducing degradation in natural forests is necessary for carbon stock resilience, than that selecting the more biodiverse of those natural forests is necessary. This results from the limitations of the existing research, rather than negative evidence about the role of biodiversity – indeed, there is a significant body of theory and evidence from other terrestrial ecosystems that indicates that forest biodiversity is likely to have a role in enhancing carbon stock resilience.

A risk-averse strategy to promote permanence of forest carbon stocks would therefore focus REDD+ efforts on natural forests before plantations, and on the more biodiverse of those forests before the less biodiverse forests. This strategy takes account of the evidence that we do have on the relationship between biodiversity and resilience. Retaining and restoring natural forests appears more likely to be a successful long-term strategy for REDD+.

It is also crucial to remember the role of forest management and context in promoting forest carbon stock permanence, which is outside the scope of this review. Management of fire hazard in forest and the surrounding landscape will be increasingly relevant as temperatures rise (e.g. Aragão and Shimabukuro 2010). In plantations, careful selection of the mixture and planting patterns of tree species used can increase both productivity and resilience (Gadgil and Bain 1999; Bodin and Wiman 2007; Schaberg *et al.* 2008), although there is much still to learn here in tropical forestry, with monoculture plantations being by far the most numerous type (Erskine *et al.* 2006).

The findings on degradation have clear implications for national REDD+ strategies: control and monitoring of deforestation alone is not enough. Deforestation is largely driven by the agricultural sector, and so may appear an easier issue to tackle than forest fragmentation and degradation, whose direct drivers can include agriculture, forestry, infrastructure development, fuelwood collection and so on. However, if deforestation is prevented but degradation is not, the indications are that the long term carbon storage function of the ‘saved’ forests will be at greater risk.

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6 Glossary

Biodiversity – “the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (UN 1992). Most of the papers that we have reviewed use species-based biodiversity measures.

Diversity-stability hypothesis – “species diversity mediates community functional stability through compensating interactions to environmental fluctuations among co-occuring species” (McNaughton 1977)

Ecosystem functioning – “a broad term that encompasses a variety of phenomena, including ecosystem properties [“sizes of compartments (e.g., pools of materials such as carbon or organic matter) and rates of processes (e.g., fluxes of materials and energy among compartments)”], ecosystem goods [“those ecosystem properties that have direct market value. They include food, construction materials, medicines, wild types for domestic plant and animal breeding, genes for gene products in biotechnology, tourism, and recreation”], and ecosystem services [“those properties of ecosystems that either directly or indirectly benefit human endeavours, such as maintaining hydrologic cycles, regulating climate, cleansing air and water, maintaining atmospheric composition, pollination, soil genesis, and storing and cycling of nutrients (Christensen et al. 1996, Daily 1997).”]” (Hooper et al. 2005)

Functional diversity – “the value and range of functional traits of the organisms present in a given ecosystem. The value of traits refers to the presence and relative abundance of certain values (or kinds) of leaf size, nitrogen content, canopy heights, seed dispersal and dormancy characteristics, vegetative and reproductive phenology, etc. The range of traits refers to the difference between extreme values of functional traits, for example, the range of leaf sizes, canopy heights, or rooting depths deployed by different plants in an ecosystem.” (Diaz and Cabido 2001)

Functional group/functional type – a set of species that have similar effects on a specific ecosystem process or similar responses to environmental conditions (Hooper et al. 2005); “the set of organisms sharing similar responses to the environment (e.g. temperature, water availability, nutrients, fire and grazing) and similar effects on ecosystem functioning (e.g. productivity, nutrient cycling, flammability and resilience)” (Diaz and Cabido 2001)

Functional redundancy – “when several species in a community carry out the same process, such as nitrogen fixation. The larger the number of functionally similar species in a community, the greater the probability that at least some species will survive changes in the environment and maintain the functional properties of the ecosystem (Walker 1992); (Chapin *et al.* 1996); (Naeem and Li 1997)).” (Diaz *et al.* 2005)

Functional traits – the characteristics of an organism that “influence ecosystem properties or species’ responses to environmental conditions” (Hooper *et al.* 2005) e.g. canopy height and structure, ability to resprout (Diaz and Cabido 2001)

Insurance hypothesis – "larger numbers of species should enhance ecosystem reliability" (Naeem and Li 1997); "increasing biodiversity insures ecosystems against declines in their functioning caused by environmental fluctuations" (Yachi and Loreau 1999)

Overyielding – "…occurs when the total production of a mixed plot of two or more species exceeds the production that would have been obtained by growing the species in a monoculture."(Drake 2003)

Recovery – "the speed of return to the original structure" (Cote and Darling 2010)

Redundant species – "Complete functional redundancy only occurs if, following the removal of one species, there is density compensation among the remaining species. A complicating factor is that the different species in a guild, while all performing the same function, may respond differently to different environmental conditions. With the complete set of species, net guild abundance (or function) may remain relatively constant under a fluctuating environment. Loss of some species may well lead to an increase in abundance of others (i.e., density compensation occurs), but because the diversity of response to environmental conditions has been reduced, net guild abundance may then fluctuate more in response to environmental fluctuations" (Walker 1992)

Reliability – "the probability that a system will provide a consistent level of performance over a given unit of time" (Naeem and Li 1997)

Resilience – "the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks" (Walker *et al.* 2004). In this paper, we focus on the aspects of **recovery** and **resistance,** but Walker's concept of **precariousness** [how close the current state of the system is to a limit or threshold] is also relevant**.**

Resistance – "how little a measurement [such as biomass content] is changed by a given disturbance" (Pimm 1991)

Shannon-Weaver index – a biodiversity indicator taking account of both the number of unique species at a site (richness) and the evenness of their abundance (relative frequency) (Krebs 1999)

Stability – "The capacity of an ecosystem to persist in the same state." (Diaz *et al.* 2005)

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