Chapter 2

Forest biodiversity, carbon and other ecosystem services: relationships and impacts of deforestation and forest degradation

Coordinating lead author: Ian D. Thompson
Lead authors: Joice Ferreira, Toby Gardner, Manuel Guariguata, Lian Pin Koh, Kimiko Okabe, Yude Pan, Christine B. Schmitt and Jason Tylianakis
Contributing authors: Jos Barlow, Valerie Kapos, Werner A. Kurz, John A. Parrotta, Mark D. Spalding and Nathalie van Vliet

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Abstract: REDD+ actions should be based on the best science and on the understanding that forests can provide more than a repository for carbon but also offer a wide range of services beneficial to people. Biodiversity underpins many ecosystem services, one of which is carbon sequestration, and individual species' functional traits play an important role in determining ecological processes. Higher levels of biodiversity generally support greater levels of ecosystem service production than lower levels, and ecosystem properties, such as resilience, are important considerations when managing human-modified ecosystems.

Tropical forests have high levels of biodiversity yet have experienced severe impacts from deforestation and degradation, with consequent losses of biodiversity and ecosystem processes that support the provision of ecosystem services, including carbon storage. Tropical montane and dry forests are especially vulnerable. In (sub-)tropical forests recovering from major disturbances, both carbon and biodiversity increase, but recovery rates diminish over time, and recovery of biodiversity is typically much slower than that of carbon. However, (sub-)tropical secondary forests are recognised for their biodiversity conservation values and as important carbon sinks. In many cases, anthropogenic factors – such as land use change, introduction of species or barriers to dispersal – can lead to the creation of 'novel ecosystems' that are distinct in species composition and functioning. The implications of these novel ecosystems for conserving ecological integrity and provision of ecosystem services remains poorly understood.

2.1 Introduction

A sound understanding of how *ecosystems*[1] function and the role that *biodiversity* plays in these functions is essential for the management of forests in general, and under REDD+ specifically. This chapter lays the science foundation for the suggested approaches to *forest management* and recovery under REDD+ in Chapter 3. The ecology of forest systems as it applies to the relationship between biodiversity and *ecosystem services* is discussed, with an emphasis on species, ecosystems and carbon. The first section outlines key concepts necessary to understanding the links between biodiversity and ecosystem services, including *carbon sequestration*. This relationship is examined with respect to how carbon accumulates and is lost from terrestrial ecosystems with a focus on tropical and sub-tropical forests, where the majority of REDD+ activities will be undertaken. The main (sub-)tropical forest types are presented, including their values in terms of carbon and biodiversity. The last main section outlines the effects of deforestation and forest degradation on both carbon and biodiversity.

2.2 The relationship between biodiversity and ecosystem functioning

People often think of biodiversity as a list of species without necessarily considering the roles that species perform in ecosystems. However, in recent decades, there has been an improved understanding of important linkages between species and the way that ecosystems function (e.g., Diaz et al., 2005; Aerts and Honnay, 2011; Estes et al., 2011; Cardinale et al., 2011). A large body of research has examined whether or not ongoing biodiversity loss is affecting ecosystem functioning under what is referred to as the 'biodiversity-ecosystem functioning hypothesis' (B-EF). A sub-set of *ecosystem 'functions'* (also called '*processes*') are ecosystem services that benefit humans (see Section 2.3), including pollination, nitrogen-fixation and carbon storage (Diaz et al., 2005; 2006). Despite considerable debate over early experimental methods (e.g., Huston, 1997) and the relevance of biodiversity experiments for the biodiversity crisis (Srivastava and Vellend, 2005), there is now consensus that ecosystem functioning increases with increasing biodiversity (Chapin et al., 2000; Hooper et al., 2005; Balvanera et al., 2006). This relationship can be obscured by strong environmental effects (Laliberté and Tylianakis, 2012) and appears to be limited via competition for resources or other mechanisms at high levels of *species richness* (e.g., in *natural forests*) and depending on the scale (e.g., Mittelbach et al., 2001).

Biodiversity promotes functioning via three main mechanisms. The first is resource (or niche) complementarity (e.g., Loreau et al., 2001), whereby different species use different resources or the same resources in different ways, resulting in reduced competition. This positive effect of biodiversity becomes stronger when multiple resources are available (Tylianakis et al., 2008) and over large spatial and temporal scales because species partition resources in space or time (Cardinale et al., 2004; Zhang et al., 2011). Complementarity depends on species performing functions in different ways, thus, the strongest increase in functioning is observed when species have different functional traits (Diaz and Cabido, 2001; Fontaine et al., 2006; Hoehn et al., 2008). Furthermore, there is evidence that turnover of species among regions (Loreau et al., 2003) and evenness in the abundance of different species (Crowder et al., 2010) also promote ecosystem functioning. The second mechanism is facilitation, whereby species provide resources or alter the environment (e.g., legumes), enabling other species to perform better (Cardinale et al., 2002; Kelty, 2006). Facilitation is often used as a silvicultural tool to grow desired shade-tolerant tree

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[1] All terms that are defined in the glossary (Appendix 2), appear for the first time in *italics* in a chapter.

species beneath faster growing pioneer tree species. The final mechanism is the 'sampling effect', whereby there is a higher probability that a high *productivity* species will be included in a large group of species compared to a smaller group (e.g., Cardinale et al., 2006). Thus, individual species effects differ and are highly important (e.g., Diaz and Cabido, 2001; Kelty, 2006; Diaz et al., 2007) and so the loss of key species can impede forest functioning (Baker et al., 2003; Lewis, 2009).

While recent studies show that diversity of *native species* enhanced grassland productivity more than *introduced species* diversity (Isbell and Wilsey 2011), there is growing recognition of the importance of species traits (Diaz and Cabido, 2001; Fontaine et al., 2006; Hoehn et al. 2008), rather than identities, to the provision of services, suggesting that some '*novel ecosystems*' (Hobbs et al., 2006; Ewel and Putz, 2004) comprised of new species assemblages may function adequately. Therefore, the functional argument for biodiversity conservation does not necessarily depend on reinstating previous ecological conditions, although provisioning, cultural, aesthetic and other benefits or services are often enhanced by native biodiversity (see Section 2.3).

2.2.1 Biodiversity and ecosystem resistance and resilience

The ability of an ecosystem to withstand environmental change, maintain its structure and composition of species (i.e., its state), and support the provision of *services* consistently over time is referred to as '*ecosystem stability*'. The term 'stability' encompasses a suite of measures (Ives and Carpenter, 2007) including the ability of a system to remain unchanged in the face of chronic perturbations (i.e., '*resistance*') and its ability to return to its original state after being altered (i.e., '*resilience*') (Ives and Carpenter, 2007), although with considerable variation in rates of processes over time. In forests, stability varies among types and especially over space, but usually refers to the recognisable mix of dominant tree species (e.g., Drever et al., 2006; Thompson et al., 2009). Ecosystem stability enables some prediction of responses to management but also suggests that *ecological thresholds* exist, beyond which the system may become unstable and shift to alternate stable states (Andren, 1994; Scheffer et al., 2001; Groffman et al., 2006), with unpredictable outcomes that may produce different or reduced services (e.g., Grau et al., 2003; Chazdon, 2003; Lewis, 2009).

Functional *redundancy* among species or genotypes can help to buffer the impacts of environmental changes (Walker, 1992; Lavorel, 1999; Yachi and Loreau, 1999; Hughes and Stachowicz, 2004), and thereby help to maintain ecosystem functioning in the face of disturbance (e.g., Elmqvist et al., 2003). This redundancy also means that some species may be lost with limited effects on functioning (Walker, 1992). The strength of the buffering capacity depends on the abilities of individual species to respond to environmental fluctuations, the specific nature of their responses and the number of species (i.e., Yachi and Loreau, 1999; Elmqvist et al., 2003; Winfree and Kremen, 2009). Buffering capacity is further affected by the condition of the ecosystem (Thompson et al., 2009): degraded systems often have reduced species richness and can have lower resilience than systems with greater integrity. On the other hand, degraded *forest ecosystems* are also often highly stable. For example, degraded systems dominated by *invasive alien species* (i.e. *Acacia* spp.) in South Africa produce greatly reduced goods and services compared to natural forests, but are highly stable and very resistant to change (van Wilgen et al., 2001).

Resistance refers to the capacity of the system to maintain its state under chronic small-scale perturbations. Some studies have suggested limited or no relationship between resistance and *species diversity* (e.g., DeClerck et al., 2006), others have suggested a positive effect (Proença et al., 2010; Royer-Tardif et al., 2010). Differences in population responses across species may produce an averaging effect that stabilises overall community functioning (Yachi and Loreau, 1999). Hence any effects of increasing biodiversity on resistance may be ecosystem-dependent and are uncertain.

Ethiopian montane forest with tree ferns.
Photo © Christine B. Schmitt

There is, however, a positive relationship between diversity (genetic, species and landscape-level) and ecosystem resilience (i.e., recovery after a major disturbance) (Pfisterer and Schmid, 2002; Griffen et al., 2009; Thompson et al., 2009; van Ruijven and Berendse, 2010). It is likely that functional diversity, not total species richness, is most relevant to ecosystem resilience (Diaz and Cabido, 2001; Fitter et al., 2005; Laliberté et al., 2010). Forest resilience is of particular interest owing to current *climate change* effects on forest processes and on carbon storage, and the resulting feedbacks to climate change. More diverse forests are generally more resilient than forests with lower diversity, on similar sites (reviewed in Stone et al., 1996; Thompson et al., 2009). This resilience is, in part, because interactions within communities play a key role in determining the stability of the ecosystem as a whole (e.g., Balvanera et al., 2006), such as via redundancy in food web interactions (Laliberté and Tylianakis, 2010). Catastrophic impacts on ecosystems following large disturbances can be mitigated by ensuring diversity at landscape scales, since different stand types will exhibit different levels of *vulnerability* (e.g., Gunderson and Holling, 2002; Peterson, 2002). These findings suggest that the structure of entire landscapes should be considered for ecosystem management in order to maximise spatial and temporal insurance (Loreau et al., 2003; Tscharntke et al., 2005). Finally, genetic diversity can also provide a considerable contribution to ecosystem resilience (Gregorius, 1996; Hughes and Stachowicz, 2004; Reusch et al., 2005). Thus, resilience is an emergent property of forest ecosystems conferred at multiple scales, through genetic, species and landscape heterogeneity (Thompson et al., 2009).

2.2.2 Ecological thresholds and safe operating space for management

Environmental change and human activities that cause local extinctions of species and alter key ecological processes may destabilise a forest ecosystem (e.g., Folke et al., 2004; Ims et al., 2007). For example, loss of species in systems can have large consequences that result in *trophic cascades*, significantly altering ecosystem structure and function (e.g., Morris et al., 2005; Estes et al., 2011). Often, ecosystem responses to environmental change may be undetectable until an *ecological threshold* is passed, resulting in non-linear and unexpected changes that may be irreversible (Andren, 1994; Scheffer and Carpenter, 2003; Folke et al., 2004; Pardini et al., 2010). Over long enough time periods or under human manipulation, ecosystems move to alternate stable states that reflect new environmental conditions (e.g., Gunderson, 2000) and may be difficult to recover (e.g., van Wilgen et al., 2001; Chazdon, 2003; Fukami and Lee, 2006), as will undoubtedly be the case under current climate change (e.g., Fischlin et al., 2009). Managing ecosystems within a 'safe operating space' ensures that they do not reach such irreversible levels of change. There are many examples of forest recovery to new states following *degradation* and these 'novel' systems may or may not provide the same ecosystem goods and services as past forests (e.g., Richardson, 1998; van Wilgen et al., 2001; Chazdon, 2003; Grau et al., 2003; Lewis, 2009).

2.2.3 The relationship between forest area and biodiversity

Several models and theories have helped to improve our understanding of the relationship between biodiversity and land use change (MacArthur and Wilson, 1967; Hanski, 1998; Ricketts, 2001). In particular, the 'power model' (Arrhenius, 1920), one of several alternative models used to describe the relationships between species and area (Tjørve, 2003), has been widely applied to predict biodiversity losses driven by deforestation (Brooks and Balmford, 1996; Brooks et al., 2002; Brooks et al., 2003). The 'species-area model' has undergone some recent improvements to better reflect real land use changes. In particular, the differential responses of species to the landscape matrix (i.e., land uses that have replaced original forests), the effects of *forest fragmentation* and *edge effects* can now be modelled and predicted (e.g., Koh and Ghazoul, 2010; Koh et al., 2010). These theoretical considerations formalise the almost ubiquitous observation that large contiguous forest areas contain more biodiversity (especially species) than smaller and isolated stands. This pattern, coupled with current knowledge on the relationships between biodiversity and the provision of ecosystem goods and services (Section 2.3), including carbon storage and sequestration (Section 2.3.1.), reinforces the value of conserving or restoring large areas of forest to improve mitigation of forest biodiversity loss, and conservation and enhancement of *carbon stocks* (see Chapter 3).

2.3 The relationship between biodiversity and ecosystem goods and services

There are four broad categories of ecosystem services: provisioning, such as production of fibre, food and water; regulating, such as climate regulation, erosion control and pollination; supporting, such as nutrient cycling, soil formation and primary productivity; and cultural, such as spiritual and recreation benefits (MA, 2005; Diaz et al., 2005). Biodiversity is related to the provision of many of these services (Turner et al., 2007). Several studies have established explicit links between biodiversity and: pollination (Fontaine et al., 2006; Hoehn et al., 2008; Tylianakis et al., 2008), predation (Ives et al., 2005; Snyder et al., 2006; Tylianakis et al., 2008), decomposition and other soil processes (Naeem et al., 1994; Culman et al., 2010; Laliberté and Tylianakis, 2012), and *biomass* production in forests (e.g., Wardle et al., 2012). The economic value of these services has been quantified in some cases (Thompson et al., 2011), for example, the global biological control of crop pests by natural enemies is estimated to be worth USD 4.5 billion per year (Losey and Vaughan, 2006). Other services, however, such as regulation of erosion and water purification are only weakly related, or unrelated, to species diversity (MA, 2005; Dobson et al., 2006) but rather depend on the type of ecosystem and its condition (Table 2.1).

A general characteristic of ecosystem services that are strongly related to biodiversity is that the key processes occur at local scales (e.g., pollination, biological control of pests, soil formation), whereas ecosystem services and goods to which biodiversity contributes less (e.g., water quality, erosion control, oxygen production) tend to operate at larger landscape to regional scales (MA, 2005; Kremen, 2005; Maass et al. 2005; Guariguata and Balvanera, 2009).

Integrated, multiple use landscape management, (see Section 2.5.5), can maintain much of the local forest

Table 2.1

Species richness and biodiversity relationship to ecosystem services

Ecosystem service	Mechanism/management effects on service	Relationship w/species richness
Erosion control	Coverage of soil surface; soil retention on slopes (Pimentel et al. 1995)	None to low
Nutrient cycle	Photosynthesis, nitrogen fixation, food-web, decomposition (CO_2 is not included here - Vitousek and Sanford, 1986; Bonan and Shugart, 1989)	medium to high (Giller, 1995; Pimentel et al., 1995; Foley et al., 2005 ; Diaz and Cabido, 2001; Eisenhauser et al., 2011; Wardle et al., 1997 ; Hättenschiler, 2005)
Natural hazard prevention: flooding	Interception of rainfall and evaporation of water infiltration by soil (FAO and CIFOR, 2005; Guillemette et al., 2005; Bruijinzeel, 2004)	None to low (Bruijinzeel, 2004)
Air quality regulation	Air filtration by plants (Givoni, 1991; Weathers et al., 2001; Bolund and Hunhammar, 1999)	Low (Givoni, 1991; Bolund and Hunhammar, 1999)
Climate regulation	Regulation of moisture in air, prevention of greenhouse gas emission (e.g. Houghton et al., 2001; Bolund and Hunhammar, 1999)	Low (Ellison et al., 2005)
Water purification and fresh water supply	Purification from polluted/contaminated to fresh water (Neary et al., 2009; Foley et al. 2005; Postel and Thompson, 2005)	Low
Disease regulation	Vector regulation, relative (lower) density of host in ecosystem/ community to regulate density of pathogens (LoGiudice et al., 2003)	High (LoGiudice et al., 2003)
Cultural services including cultural diversity and identity, recreation and ecotourism, and education	Provisioning of landscape (scenery); Symbolic (flagship) species	High but different locally
Food, fibre, timber production	Harvest and cultivation	Low to high (Thompson et al., 2009; Cardinale et al., 2011)
Pollination	Pollen transfer by animals (insects, birds) (e.g. Ricketts, 2004); forest habitat required for pollinators and depends on movement capability and landscape pool of pollinators (Kremen et al., 2004; Tscharntke et al., 2005; Tylianakis et al., 2008)	High (Kremen et al., 2002; Ricketts, 2004; Greenleaf and Kremen, 2006; Hoehn et al., 2008; Tylianakis et al., 2008)
Biological pest control	Requires habitat for natural enemies (Landis et al., 2000), predator diversity can depend on the environmental context (Terborgh et al., 2001; Tylianakis et al., 2008; Tylianakis and Romo, 2010)	High (Ives et al., 2005; Snyder et al., 2006 ; Tylianakis et al., 2008; Tylianakis and Romo, 2010)
Seed dispersal	Fruit feeding and dispersal of seeds, usually by birds or mammals (Tscharntke et al., 2008); diversity of dispersers can improve provision of this service (Garcia and Martinez, 2012).	None (wind) to high (animals) (Garcia and Martinez, 2012)

biodiversity and provide the agents necessary for certain ecosystem services, such as pest control and pollination, thereby resulting in both sustainable agriculture and forestry (Tscharntke et al., 2005; Kleijn et al., 2006; Koyanagi et al., 2009). In contrast, large-scale intensive land conversion for timber, pulpwood or agricultural crops can degrade natural ecosystems (Matson et al., 1997; Lambin et al., 2001; Tilman et al., 2002).

2.3.1 Biodiversity and carbon sequestration and storage in forests

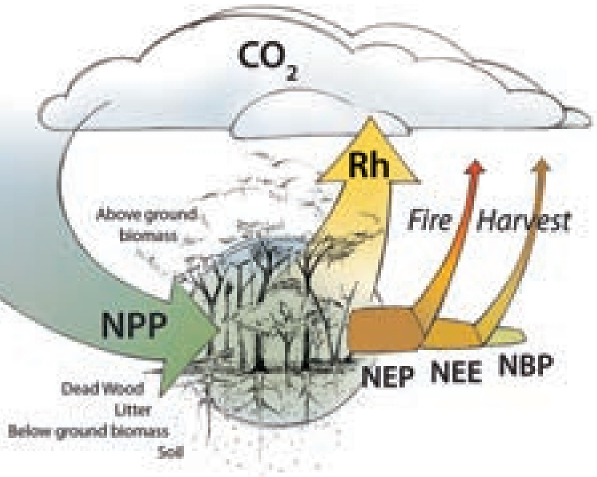
The sequestration and storage of carbon is one of the many ecosystem services supported by biodiversity. Carbon is initially sequestered through photosynthesis before being transferred to one of a number of terrestrial pools including *above-ground biomass* (AGB), *dead wood*, litter, roots (*below-ground biomass)* and soil (Figure 2.1). These pools are then subject to gains and losses depending on rates of growth, mortality and decomposition that are in turn affected by varying human and natural disturbances. Species can affect the long-term balance of carbon gains and losses in ecosystems through different components of the *carbon cycle*, including the magnitude, turnover and longevity of carbon stocks in soils and vegetation (Díaz et al., 2009; Murphy et al., 2008; Barantal et al., 2011; Maestre et al., 2012). Experiments with tree *plantations* of native and introduced species have often found significant and positive effects of species richness on different components of the carbon cycle, including productivity (e.g., Piotto, 2008; Healy et al., 2008), decomposition (Scherer-Lorenzen et al., 2007), soil respiration (Murphy et al., 2008) and plant mortality (Healy et al., 2008). Studies have shown that, under similar conditions, tree plantations with two or more species may achieve higher levels of productivity than single-species plantations for a range of species combinations, if species' mixes involve complementary resource use (i.e., stratified canopy structures) and/or facilitation of tree growth of one species by the other (Piotto, 2008; Forrester et al., 2006; Kelty, 2006) (see also Chapter 3, Section 3.2.4).

While a positive relationship between tree species richness and above-ground productivity has often been found (Thompson et al., 2009; Nadrowski et al., 2010; Potvin et al., 2011, Annex 2.1), this relationship is not universal (Mittelbach et al., 2001; Thompson et al., 2009). For example, no relationship was found between species richness and either above-ground or below-ground biomass or litter in naturally regenerating conifer stands in China, ranging from 5 to 310 years (Zhang et al., 2011), and no significant relationship was found between productivity and diversity in plantations in Australia where stands varied from 23 to 72 years (Firn et al., 2007). Nevertheless, a majority of the studies assembled in Annex 2.1 suggested a positive relationship between species richness and some aspect of forest *production* or respiration, and Zhang et al. (2012) found a positive relationship in multiple studies via meta-analysis. There are also non-linear landscape-level effects because changes in ecosystem processes are affected by the fragmentation of forests and edge effects that exacerbate species loss, population decline and ecosystem functioning (e.g., Laurance et al., 2007).

The majority of studies have not distinguished the effects of species composition on productivity and other ecosystem functions, from the effects of species richness or individual species. However, a significant positive effect of species composition, but not of species richness, was found for litter decomposition rates in rainforests (Giesselmann et al., 2010; Barantal et al., 2011). By contrast, a greater effect of species richness than species composition was reported in a natural tropical forest in Panama (Ruiz-Jaen and Potvin, 2010). The latter study reported that differences in plant species richness were more important in explaining patterns of carbon storage

The major carbon fluxes in forest ecosystems

Figure 2.1



Net Primary Production (NPP) quantifies the amount of organic matter produced annually. Most of this carbon uptake is offset through losses from the decomposition of litter, dead wood and soil C pools (Rh = heterotrophic respiration). The net balance (Net Ecosystem Production, NEP) is further reduced through direct fire emissions to yield Net Ecosystem Exchange (NEE), from which harvest losses are subtracted to estimate the annual C stock change in forest ecosystems (Net Biome Production, NBP). Positive NBP indicates increasing forest carbon stocks, a sink from the atmosphere, while negative NBP indicates a carbon source. NEE is reported from the perspective of the atmosphere and has the opposite sign convention.

Figure provided by Avril Goodall, CFS.

than changes in plant species composition or relative species dominance (Annex 2.1). In relatively simple forest systems, individual species may dominate processes, and in complex systems, certain species and *functional groups* are often particularly important in controlling specific processes (e.g., Baker et al., 2003; Diaz et al., 2007; Aerts and Honnay, 2011). Greater clarification of the importance of individual species effects, and the role of functional groups for carbon storage is an important area for further research.

2.4 Biodiversity and carbon in major (sub-)tropical forest types

2.4.1 Definition and distribution of (sub-) tropical forest types

A number of forest types can be described in the tropical and sub-tropical regions where REDD+ activities could take place (see map in Chapter 1, Figure 1.1). According to FAO definitions (2001), the tropical domain is located between the Tropics of Cancer and Capricorn (23°N to 23°S) with mean annual temperatures above 18°C. The sub-tropical domain is located between 25° and 40° north and south of the equator and the temperature is above 10°C for at least eight months of the year. The domains are further divided into ecological zones mainly based on climatic factors (Figure 1.1; FAO, 2001). For simplification and for the purposes of this assessment report, the different tropical and sub-tropical ecological zones that contain forests were combined into three major forest types: tropical rainforests, (sub-)tropical dry forests and woody savannahs, and (sub-)tropical montane forests (Table 2.2). Mangroves and freshwater swamp and peat forests are discussed separately because of their particular importance for carbon storage. The latter occur in several (sub-)tropical ecological zones. While there are estimates of the global extent of mangrove forests, the area of freshwater swamp and peat forests is uncertain (Page et al., 2010; Table 2.2). Among the different (sub-)tropical forest types, rainforests cover the largest area (at a 25 percent tree cover threshold), including primary and *secondary forests* (see Annex 2.2).

Different definitions and measurements of (sub-)tropical forest area and types render a detailed comparison across studies difficult (e.g., Mayaux et al., 2005; Schmitt et al., 2009; Mace et al., 2005). Crucial methodological differences are related to the identification of woody land cover other than natural forest and the use of different tree cover thresholds (between 10 and 40 percent) that influence the estimation of extent, especially for (sub-)tropical dry forests and savannahs (Schmitt et al., 2009; Miles et al., 2006). For instance, the tropical dry forest area of 707 Mha estimated by Mayaux et al. (2005) is much larger than the 458 Mha identified in Table 2.2. Furthermore there are many other different global ecosystem classifications, such as the Global Land Cover 2000 classes (see Mayaux et al., 2005) and the WWF ecoregions, based on bio-geography and species assemblages (Olson et al., 2001; Mace et al., 2005). There are also many finer-scaled forest classifications, using plant species composition and environmental factors that were developed for the sub-national (e.g., Clark and Clark, 2000; Cannon et al., 2007) or national level (e.g., Friis et al. 2010; Letouzey, 1985).

2.4.2 Spatial patterns of biodiversity in (sub-) tropical forest types

There is broad consensus that species richness is generally highest in tropical rainforests compared to all other (sub-)tropical forest types (Table 2.3; Mace et al., 2005). However, species richness is only one aspect of biodiversity, and it is crucial to consider species composition, species distributions and the differences in species composition across similar forest types but in different regions of the world. For example, there are notable differences in the vascular plant and vertebrate species richness among the tropical rainforests of Africa, Asia and South America. In addition, there are areas of extremely high vascular plant and vertebrate species richness in tropical montane forests and the number of tree species is higher in (sub-)tropical moist montane forests than in (sub-)tropical moist lowland forests (Table 2.3).

Endemism is very high in (sub-)tropical forests but patterns of species richness and endemism are not congruent among all continents or major forest types (Gentry, 1992; Orme et al., 2005; Ghazoul and Sheil, 2010). While high diversity tropical rainforests are concentrated in lowland areas, with high and evenly distributed rainfall, the highest rates of endemism occur in isolated cloud forests, topographically dissected montane areas and on islands or other isolated forest areas (Gentry, 1992). Perhaps the best available data are for birds, which indicate that 32, 24 and 15 percent of global endemic avian species occur in tropical lowland moist, tropical montane moist and tropical dry forests, respectively (Stattersfield et al., 1998). Many (sub-)tropical forest areas are recognised as global biodiversity ‘hotspots’ because they feature exceptional concentrations of endemic species and are experiencing exceptional loss of *habitat* (Myers et al., 2000; Mittermeier et al., 2004; Schmitt et al., 2009). For example, Hubbell et al. (2008) suggested that there are over 11,000 tree species in the Amazon region, but at current rates of deforestation, forest degradation and climate change, at least 1,800 to 2,600 species are predicted to become extinct in the next few decades. In fact, habitat change and loss are the major reason for all groups of species to be listed as vulnerable and endangered on the IUCN Red List of Threatened Species (Vié et al., 2009). (Sub-)tropical moist montane, (sub-)tropical moist lowland and (sub-)tropical dry forests contain the greatest percentage of species affected for all taxa (32, 22, and 22 percent, respectively) (Table 2.3).

Tropical rainforests

The global distribution of tropical rainforests is primarily determined by climatic conditions such as uniformly high temperatures, high precipitation of at least 1,500 mm yr^{-1} (but mostly between 2,000 and 3,000 mm yr^{-1}) and a

Table 2.2

Forest area and above-ground biomass (AGB) carbon for the five major forest types in the tropical and sub-tropical domain based on the Saatchi et al. (2011) tropical above-ground biomass map, the FAO ecological zones (Figure 1.1; FAO, 2001) and the MODIS forest cover map (25 percent forest cover threshold) (NASA, 2010). Carbon is defined as 50 percent above-ground biomass. SD is the standard deviation of spatial variations of estimates across the regions. For area and carbon data by region and ecological zone see Annex 2.2.

	Tropical rainforests	**(Sub-) tropical dry forests and woody savannahs**	**(Sub-) tropical montane forests**[1]	**(Sub-) tropical Freshwater swamp and peat forests**[2]	**(Sub-) tropical mangrove forests**[2]
Combined FAO ecological zones	Tropical rainforest	Tropical moist deciduous forest, Tropical dry forest, Tropical shrubland, Sub-tropical dry forest	Tropical mountain systems, Sub-tropical mountain systems		
Forest area across Africa, Latin America and Southeast Asia (Mha)	1,101.6	457.9	164.2	51.9 (tropical flooded forests, Mayaux et al., 2005)[3]	15.2 (global mangrove forests, FAO, 2007; Spalding et al, 2010)
AGB carbon density (Mg C ha^{-1} ± SD)	115 ± 79	53 ± 121	94 ± 87	not known (NB: high below-ground carbon density)	not known (NB: high below-ground carbon density)
Total AGB carbon across Africa, Latin America and Southeast Asia (10^6 Mg)	126.1	24.4	15.5	not known	not known
Examples	Amazon Basin, Congo Basin	Cerrado (South America), Miombo (Africa)	Eastern African mountains, Eastern Himalayas	Brazil, Borneo, Sumatra	Gulf of Guinea (Africa), Greater Sundas (Asia)

NB: The sub-tropical humid forests are not included in this summary table because they encompass a wide range of forest ecosystems from evergreen broadleaved forest in Southeast China to coniferous forest in Brazil and bushland in southern Africa. For area and carbon data see Annex 2.2.

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[1] Mountain systems are located at > 1,000-1,500m elevation (FAO, 2001)

[2] These are azonal forest types that can occur within the other FAO ecological zones and are not mapped out explicitly (Figure 1.1; FAO, 2001). Area data are from other sources as indicated.

[3] Area of tropical forest regularly flooded by freshwater and saline water (10 percent tree cover threshold); includes mangrove forests but peat forests probably underestimated (e.g. Page et al., 2010).

short or absent dry season (see map in Chapter 1, Figure 1.1; FAO, 2001). Competition for light is the primary driver of vegetation dynamics and structural complexity (Murphy and Bowman, 2012). The high species diversity of tropical rainforests renders small-scaled classification of forest types complex (Leigh et al., 2004; Ghazoul and Sheil, 2010).

There are notable differences in rainforest species diversity among the continents. For example, there is high bird and bat species richness and many Bromeliads mostly in the Neotropics, while most diversity of gliding animals and dipterocarp trees occurs in Southeast Asia. The estimated number of rainforest plant species also varies, with 93,500, 61,700, and 20,000 species in the Neotropics, the Asia-Pacific region and Africa (including Madagascar), respectively (Corlett and Primack, 2011). These differences are related to continental drift, differences in rainfall and its seasonal distribution, and extinctions caused by past natural and anthropogenic environmental changes (Corlett and Primack, 2011; de Gouvenain and Silander, 2003; Parmentier et al., 2007). Within the tropical rainforest regions, lower species diversity occurs where there is annual rainfall under 2,000 mm yr^{1}, a pronounced dry season, periodic flooding, and sandy or peat soils (FAO, 2001; Corlett and Primack, 2011).

(Sub-)tropical dry forest and woody savannahs

(Sub-)tropical dry forest and woody savannahs contain several ecological zones (Table 2.2), characterised by a distinct dry season of at least three, but up to eight,

Table 2.3

Numbers of species by selected species groups and major (sub-) tropical forest types from IUCN (www.redlist.org) that have been assessed, and total species numbers in vulnerable (=VU) or higher categories (critically-endangered and endangered = EN).

Major forest type	Mammals		Birds		Amphibians		Reptiles		Trees	
	all sp.	EN/VU	all sp.	EN/VU	all sp.	EN/VU	all sp.	EN/VU	all sp.	EN/VU
(Sub-) tropical dry	1014	179	1853	161	422	93	642	137	694	452
(Sub-) tropical moist lowland	2259	511	5045	557	2946	724	934	191	1131	732
(Sub-) tropical mangrove	172	61	912	62	15	2	47	9	10	4
(Sub-) tropical swamp	268	70	688	44	132	15	27	3	65	14
(Sub-) tropical moist montane	1551	417	3627	450	2831	1197	627	129	1479	1085

NB: There are some differences between the way forests are classified under the IUCN Red List and the FAO global ecological zones (Figure 1.1). For example, Brazilian cerrado and African miombo woodlands are classed mostly as savannah ecosystems under the IUCN, while FAO (2001) includes these woodland types with tropical moist deciduous and tropical dry forests. Thus, the (sub-) tropical dry forests and woody savannahs (Table 2.2) are actually more species rich than the IUCN (sub-) tropical dry forest in this Table would suggest.

months and annual rainfall mostly below 1,500 mm yr^{-1} (FAO, 2001). In addition to climate, the distribution of these forest types is governed by soil fertility and fire frequency (Murphy and Bowman, 2012). There are areas of dense (sub-)tropical dry broadleaf forest where soils are relatively fertile but where long dry periods, or decadal scale droughts, occur, e.g., the monsoon forests of mainland Southeast Asia, the Atlantic dry forests of Brazil and the coastal forests of Southern and Eastern Africa (Olson et al., 2001; Burgess and Clarke, 2000; FAO, 2001). These forests are often species rich with many endemics; in Mexico, the dry broadleaf forests contain about 6,000 vascular plant species, of which 40 percent are endemic (FAO, 2001).

Madagascar montane forest
Photo © Christine B. Schmitt

Where soils are less fertile or extended dry periods more frequent, (sub-)tropical dry forests can structurally resemble woody savannahs, but lack a significant grass component (Grace et al., 2006; Vieira and Scariot, 2006; Pennington et al., 2009). Areas of varying forest cover are often closely interconnected with savannahs, whose distribution is determined by a poorly understood combination of nutrient-poor soils, natural or anthropogenic fires, and wild or domestic animal grazing (Murphy and Lugo, 1986; Murphy and Bowman, 2012; Prance, 2006). An example is the Brazilian *cerrado* (a mosaic of grasslands, savannah, woodlands and patches of gallery forest), where growth of closed dry forest is inhibited by low soil fertility, despite relatively high annual rainfall (Grace et al., 2006). In Central and Southern Africa, the structurally similar woody savannahs are characterised by the *Brachystegia* (miombo woodlands) (Prance, 2006; Shirima et al., 2011). Both the *cerrado* and the miombo woodlands harbour large numbers of endemic species (Mittermeier et al., 2003; 2004).

(Sub-)tropical montane forests

(Sub-)tropical montane forests are located between 1,000 and about 4,000 m, and support different forest ecosystems along altitudinal belts from evergreen sub-montane rainforest to cloud forest (Figure 1.1; FAO, 2001). Generally, forest canopy height declines with increasing altitude; the (sub-)tropical timberline (where shrubs and grasslands dominate) depends on climate and anthropogenic influence but is located at 3,000-4,000 m (e.g., Bussmann, 2004; Friis et al., 2010; Kessler, 2000).

Regions of high spatial heterogeneity, such as the mountainous areas of the humid tropics and sub-tropics support high biodiversity, including many endemic species (Mace et al., 2005; Gentry, 1992). For instance, the tropical broadleaf forests in the mountains of Costa Rica have an estimated 10,000 vascular plant species per 10,000 km^2 (Olson et al., 2001). Conifer montane forests occur in Mexico and Central America, the Himalayas and the dry forests of Ethiopia (FAO, 2001). Many of the (sub-)tropical mountain areas are designated as biodiversity hotspots (Myers et al., 2000; Mittermeier et al., 2004) including in the tropical Andes and the montane regions of Eastern Africa (Schmitt et al., 2009).

(Sub-)tropical freshwater swamp and peat forests

Freshwater swamp forests are characterised by waterlogged soils (FAO, 2001). Globally, they are most extensive in the Amazon basin where two types occur: *igapo* that is more or less permanently flooded swamp forest, and *várzea* that is seasonally flooded with relatively rich soils (Butler, 2011). Other areas occur in the Congo River basin, New Guinea and Southeast Asia. Peat and swamp forests generally support a lower diversity of plants than other rainforests on drained land because plants need special adaptation mechanisms for seasonal water extremes (Corlett and Primack, 2011; FAO, 2001). Peat forests occur on raised, deep peat beds where the forest is isolated from ground water and are particularly extensive on the islands of Borneo, Sumatra and New Guinea. The Amazonian peatland is also significant in area (Lähteenoja et al., 2009; Page et al., 2010). Height and species diversity of the vegetation decreases with increasing peat depth, and forests can be dominated by one species, such as the *alan* peat swamp forests of Borneo dominated by light red meranti (*Shorea albida*) (Corlett and Primack, 2011; FAO, 2001; Rieley and Page, 1997).

(Sub-)tropical mangrove forests

Mangrove forests are formed by a highly specialised group of trees and shrubs that thrive in saline, tidally flooded soils, along (sub-)tropical coasts and estuaries (Spalding et al., 2010; Giri et al., 2011) and have a simple structure and relatively low plant diversity (Corlett and Primack, 2011). At least 73 mangrove species and hybrids are recognised worldwide, with 38 common species. Highest richness of mangroves is concentrated in a core area around insular Southeast Asia (Spalding et al., 2010). Many mangrove stands are dominated by few species, with distinctive communities zoned by substrate age, salinity and tidal conditions. Faunal diversity is also relatively low but the tidal influence creates a unique combination of marine, estuarine and terrestrial species (Hogarth, 2007).

Mangrove forest, Marajó, Brazil
Photo © Christine B. Schmitt

2.4.3 Spatial patterns of carbon in (sub-)tropical forest types

On average, tropical rainforests have higher above-ground biomass carbon density than the other (sub-)tropical forest types, and globally they are the largest pool of above-ground biomass carbon (Table 2.2). The data on above-ground biomass and total biomass carbon for (sub-)tropical forests by FAO ecological zones presented here is the first developed using globally consistent methods (Annex 2.2). There is a high variability in carbon density within the major (sub-)tropical forest types (Table 2.2) but also within each ecological zone (Annex 2.2), which is likely related to the inclusion of both primary and secondary forests and to the considerable variety of forest ecosystems in each ecological zone. For example, for African montane forests, above-ground biomass carbon decreases considerably above approximately 1,600 m altitude (Baccini et al., 2008; Marshall et al., 2012).

While the importance of tropical rainforests to the global carbon pool is uncontested, a detailed comparison of global carbon data is impeded by the high variability in the consideration of different carbon pools, definitions of forest types and wall-to-wall remote sensing versus plot-based studies, which are mostly not global in scale. For instance, the inconsistent use of definitions for (sub-)tropical dry forests and woody savannahs leads to a large variation in estimates of their biomass and carbon content (Becknell et al., 2012; Grace et al., 2006; Baccini et al., 2008).

A major knowledge gap remains in understanding the magnitude and dynamics of below-ground carbon stocks and fluxes in the different forest types (Lal, 2005). Saatchi et al. (2011) estimated below-ground biomass (BGB) carbon as a fraction of that above ground (Annex 2.2), a method prone to uncertainty, as for example in tropical savannahs, where carbon content below ground may exceed that above ground due to relatively high root biomass (Grace et al., 2006). Furthermore, tropical peatland forests have organic soils up to several metres deep and are among the largest terrestrial organic carbon reserves (on a ha^{-1} basis) (Lähteenoja et al., 2009). (Sub-)tropical mangrove forests can have relatively low above-ground biomass carbon but very high total carbon stocks because of their high investment in below-ground biomass and high *soil carbon* (Donato et al., 2011; Komiyama et al., 2008; Lovelock, 2008).

2.4.4 Congruence between carbon density and species richness across different scales and ecological zones

At the global scale, there is a strong positive correlation between the distribution of total biomass carbon and species richness of selected vertebrates (Strassburg et al., 2010), suggesting that tropical rainforest areas can deliver multiple benefits under REDD+ for both biodiversity and carbon objectives. However, there are also extensive areas with high species richness and lower carbon density such as (sub-)tropical mountain ecosystems (Strassburg et al., 2010). In contrast, (sub-)tropical flooded and peat forests may have lower species richness and lower above-ground biomass carbon but very high below-ground carbon density (e.g., Corlett and Primack, 2011; Donato et al., 2011; Lähteenoja et al., 2009). In (sub-)tropical dry forests and woody savannahs carbon content can be highly variable above- and below-ground, with high endemism (e.g., Grace et al., 2006; Mittermeier et al., 2003; 2004).

Spatial relationships in the distribution of carbon and biodiversity have also been investigated at the national scale, illustrating a high level of correspondence between carbon stocks and mammal species richness in Tanzania (Khan, 2011; see Figure 3.3 in Chapter 3) and different taxonomic groups in South Africa (Egoh et al., 2009). Data from Mexico illustrate the spatial pattern and relationship between biomass and vertebrate species richness at a very large scale (Figure 2.2). By contrast, at the sub-national level, carbon stocks exhibited low overlap with species richness in several South African ecosystems (forests, savannahs and grasslands) when compared to services such as water flow and soil retention at the scale of 1 km (Egoh et al., 2009). Here the spatial congruence between carbon stocks and species richness was consistently low, with values of 8, 13 and 21 percent, for mammals, birds and butterflies, respectively. Similarly, Anderson et al. (2009) and van Rensburg et al. (2002) reported that associations between carbon and biodiversity were sensitive to spatial resolution, extent and regional variation in data.

Detailed knowledge of forest types, carbon and biodiversity patterns at sub-national and national scales can help to facilitate decision-making for REDD+ investments to achieve conservation and carbon objectives (e.g., Egoh et al., 2009; Cannon et al., 2007; UNEP-WCMC et al., 2008) (see also Chapter 3).

2.5 Effects of deforestation and forest degradation on carbon and biodiversity

2.5.1 Causes of global deforestation and forest degradation

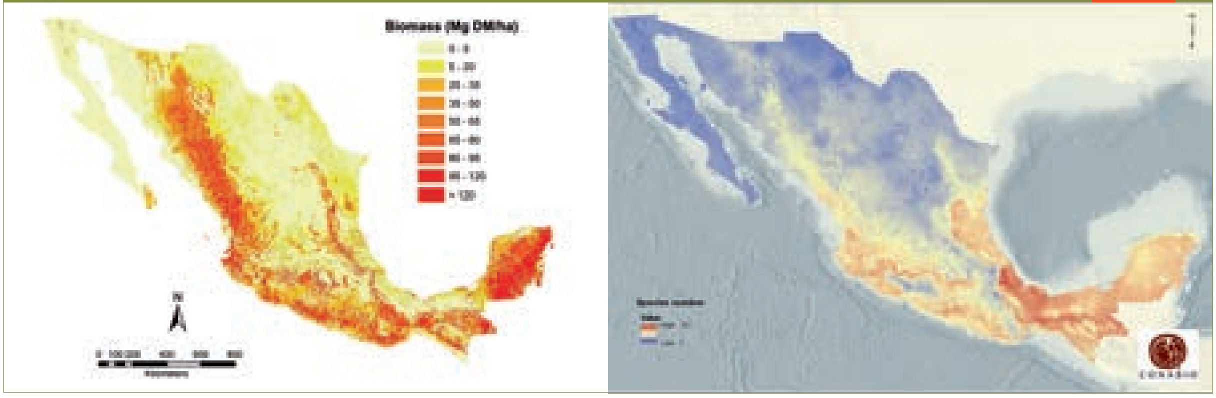
Causes of deforestation

Between 1990 and 2010, 13 to 16 million ha of forests were lost each year (FAO, 2010). Rates of deforestation are particularly high in the tropical ecological domain, with an estimated net forest loss of 8.0 million ha yr^{-1} between 2000 and 2005 (FAO, 2011). Although recent deforestation rates have fallen in some countries, continued pressure on forests would suggest that rates of forest loss in tropical and sub-tropical countries are likely to remain high in the foreseeable future (e.g., Rudel et al., 2009; FAO, 2011).

The ultimate drivers of forest loss include rapid population growth, increasing global natural resource consumption, and the often over-riding effects of economic globalisation and global land scarcity (Lambin and

Spatial patterns of vertebrate species richness and biomass carbon in Mexico

Figure 2.2



The left figure shows total biomass density (dry matter in Mg ha^{-1}) distribution (Source: de Jong and Olguin, Ecosur); the right map illustrates predictive modelling of expected vertebrate species richness (Source: CONABIO).

Meyfroidt, 2011; Kissinger et al., 2012), combined with problems of weak *governance*, inadequate policies, lack of cross-sectoral coordination, perverse incentives and illegal activities (Kissinger et al., 2012 - also see Chapter 4).

Agricultural expansion has been the most important proximate cause of forest loss, accounting for 80 percent of deforestation worldwide, with the majority occurring during the 1980s and 1990s through conversion of tropical forests (Gibbs et al., 2010). Commercial agriculture has been responsible for approximately two thirds of deforestation in Latin America, while in Africa and (sub-) tropical Asia subsistence farming is the major driver of land use change (Kissinger et al., 2012). Recent human impacts on global forest ecosystems have not been equal, with some forest types now under severe threat. Both (sub-)tropical dry and montane forests have been converted to a large extent because they are located in climates highly suitable for agriculture and grazing (Rodrigues et al., 2004; Grace et al., 2006). Mangrove forests declined by 19 percent from 1980 to 2005 (FAO, 2007), due to land clearing, aquaculture, changes to hydrological regimes and coastal development (Donato et al., 2011; Spalding et al., 2010).

Causes of forest degradation

Forest degradation can be characterised as a continuum of decline in the provision of ecosystem services resulting from increasing levels of unsustainable human impacts, relative to a more desirable condition (e.g., Chazdon, 2008; Thompson et al., in press). While deforestation represents an obvious ecosystem change, forest degradation is often more difficult to discern or quantify (Sasaki and Putz, 2009). The Collaborative Partnership on Forests (CPF) broadly defines forest degradation as "a reduction of the capacity of a forest to provide goods and services" (Simula, 2009; Thompson et al., in press). Forest may be degraded from several perspectives including productive capacity, protective capacity, biodiversity, health and carbon storage, but how these perspectives on degradation are perceived is a societal decision (Thompson et al., in press). The International Tropical Timber Organization (ITTO, 2002) has estimated that up to 850 million ha of tropical forest could already be degraded.

The proximate drivers of forest degradation include unsustainable and illegal logging, over-harvest of fuelwood and *non-timber forest products* (NTFPs), overgrazing, human-induced fires (or fire suppression in dry forests) and poor management of *shifting cultivation* (Chazdon, 2008; Kissinger et al., 2012). For example, unsustainable timber extraction accounts for more than 70 percent of forest degradation in Latin America and (sub-) tropical Asia (Kissinger et al., 2012). Unsustainable logging has resulted in forests being degraded by removal of high-value trees (Putz et al., 2011), the collateral damage associated with log extraction, and subsequent burning and clearing (Asner et al., 2006; Foley et al., 2007). Fuelwood collection, charcoal production and grazing are major causes of forest degradation, particularly across Africa (Kissinger et al., 2012). For example, the miombo woodlands of Southern and Eastern Africa provide fuelwood for approximately 100 million people (Boucher et al., 2011).

Although fire is a natural element in many forest ecosystems, humans have altered fire regimes across 60 percent of terrestrial habitats (Shlisky et al., 2009). Fires in tropical rainforests have increased in extent and frequency with the expansion of agriculture (Uhl and Buschbacher, 1985), forest fragmentation, unsustainable shifting cultivation and logging (Siegert et al., 2001; Nepstad et al., 1999; Alencar et al., 2006). Forest fires were estimated to have burned 20 million hectares of tropical forests in Southeast Asia and Latin America during 1997-1998 (Cochrane, 2003).

In addition to the detrimental impacts of land-use change and human-induced forest degradation, climate change poses an increasing threat to global forest ecosystems, in particular through an increase in the frequency of severe droughts (Malhi, 2012). (Sub-)tropical regions that appear particularly vulnerable to warming and drought include Central America, Southeastern Amazonia and West Africa (Zelazowski et al., 2011; Phillips et al., 2008).

Deforestation and forest degradation can often act synergistically. Deforestation fragments forest landscapes, which often results in degradation of remaining forests due to edge effects (e.g., drying of the forest floor, increased fire frequency, increased tree mortality and shifts in tree species composition) (Balch et al., 2008; Blate, 2005; Alencar et al., 2004; Foley et al., 2007). Poorly planned logging and deforestation increase road access to remaining forest interiors, further facilitating shifting cultivation and other land clearing, hunting, illegal logging, blowdown and fire (Foley et al., 2007; Bradshaw et al., 2009; Griscom et al., 2009; Harrison, 2011). Degradation can lead to deforestation; for example, in the Brazilian Amazon basin, Asner et al. (2006) estimated that16 percent of unsustainably logged areas were deforested during the following year, and 32 percent in the following three years. Degraded forests can often remain in a degraded state for long periods of time if degradation drivers (e.g., fire, human and livestock pressures) remain, or if ecological thresholds have been passed, and yet remain officially defined as 'forests' for classification purposes (Murdiyarso et al., 2008; Sasaki and Putz, 2009; FAO, 2010).

2.5.2 Impacts of deforestation and forest degradation on carbon

Tropical and sub-tropical forests store an estimated 247 Gt C (in biomass both above ground and below ground) (Saatchi et al., 2011). When the forest is replaced by croplands, often through burning, a large portion of carbon stored in above-ground vegetation is immediately released to the atmosphere as carbon dioxide (and other *greenhouse gases*), or over time through the decomposition of debris. Carbon in soils following deforestation can also become a large source of emissions because of increased soil respiration with warmer ambient temperatures (Bormann and Likens, 1979). There is increased soil loss with higher flooding and erosion rates, with carbon being transported downstream where a large fraction of the decayed organic matter is released as CO_2 (Richey et al., 2002).

In the last two decades, the net carbon emissions from tropical deforestation and degradation were almost equal to the total emissions from global land-use change (1.1 Pg C yr^{-1}) because effects of land-use changes on carbon were roughly balanced in non-tropical areas (Pan et al., 2011), effectively negating the role that tropical forests play as long-term *sinks* of carbon dioxide (Phillips et al., 1998; Lewis et al., 2011). Carbon emissions from forest degradation are difficult to assess because of a lack of consistent data. Forest degradation is often pooled with deforestation to estimate emissions from land-use change (e.g., Houghton, 2003), or is estimated as less than 10 percent of tropical carbon emissions (e.g., Nabuurs et al., 2007). Emissions from degradation, however, are likely to be more substantial (Putz et al., 2008; Lambin et al., 2003).

Poor logging practices create large canopy openings and cause collateral damage to remaining trees, sub-canopy vegetation and soils (Asner et al., 2006). During timber harvest, a substantial portion of biomass carbon (approximately 50 percent) can be left as logging residues, and about 20 percent of harvested wood biomass is further lost in the process of manufacturing wood products (Pan et al., 2011; Ciais et al., 2010). There is a continuing loss of carbon from oxidation of wood products, and the majority of wood products retain carbon for less than 30 years (Earles et al., 2012). Degradation of dry forests from extensive fuelwood gathering may have an impact comparable to commercial timber harvesting in rainforests (Murdiyarso et al., 2008). FAO (2006) estimated that fuelwood harvesting accounts for 40 percent of global removal of wood from forests. In recent decades, the frequency and size of forest fires have increased in many (sub-)tropical regions (Aragão and Shimabukuro, 2010), often associated with deforestation and land-use practices (Cochrane, 2003). Fire frequency may be intensified in forests that have been degraded by logging or previously burned (Holdsworth and Uhl, 1997; Cochrane, 2003), because these areas become more flammable and fire is more likely with human encroachment (Foley et al., 2007; Barlow et al., 2012).

Slash-and-burn agriculture makes a significant contribution to overall greenhouse gas emissions in tropical countries (see Chapter 3). Estimated greenhouse gas (GHG) emissions from slash-and-burn agriculture amount to 241 ±132 Tg yr^{-1} for Asia, 205 ±139 Tg yr^{-1} in Africa and 295 ±197 Tg yr^{-1} in the Americas (Silva et al., 2011).

In Southeast Asia, freshwater swamp and peat forests have been severely degraded in recent decades by unsustainable logging and agricultural expansion. Significant increases in the number of large-scale forest fires have resulted in large releases of CO_2 and non-CO_2 GHG emissions in the region (Page et al., 2002; Hooijer et al., 2010), due in particular to the high carbon content in partially decayed organic matter of peat soils (Donato et al., 2011).

The consequences of fire hazard are still poorly understood but the impact on carbon emissions is particularly significant (van der Werf et al., 2009). When measured against adjacent unburned forests, even low to medium severity fires in undisturbed or lightly degraded intact forest can kill over 50 percent of all trees (Barlow et al., 2003) and almost all of the large lianas (Cochrane and Schulze, 1999; Gerwing, 2002; Barlow et al., 2012). Trees in tropical humid forests are particularly susceptible to fire damage because fires are historically rare (Aragão and Shimabukuro, 2010; McMichael et al., 2012). In extreme drought years, carbon emissions from tropical forest fires can exceed those from deforestation (Houghton et al., 2000). For example, total estimated carbon emissions from tropical forest fires during the 1997-98 El Niño event were 0.83 to 2.8 Pg C yr^{-1} (Alencar et al., 2006; Cochrane, 2003; Page et al., 2002).

Toucans are important seed dispersers. Toco toucan (*Ramphastos toco*) in Brazil's Atlantic Forest. Photo © PJ Stephenson.

Over decadal time scales, forests can experience a loss of carbon stocks through the indirect effects of hunting of species that have functional roles, such as pollinators (e.g., large fruit bats), seed predators (e.g., peccaries, agoutis, squirrels) and seed dispersers (e.g. primates, frugivorous bats and birds) (Brodie and Gibbs, 2009; Harrison, 2011). For example, hunting in Peru has caused a shift in tree species composition as large-seeded species (which often have a high wood density; Wright et al., 2007) dispersed by large animals are replaced by smaller-seeded species, dispersed abiotically or by smaller animals (Terborgh et al., 2010; Terborgh et al., 2008). Tree growth rates and above-ground plant productivity are positively affected by red howler monkeys (*Alouatta seniculus*) (Feeley and Terborgh, 2005). Loss of these processes results in subtle but long-term cumulative degradation of forest functioning.

2.5.3 Impacts of deforestation and forest degradation on biodiversity

Deforestation and forest degradation are the two major causes of loss of biodiversity from forests (e.g., Vié et al. 2009). Conversion of forests to permanent agriculture and pasture results in an almost total loss of the original biodiversity, with reduced ecosystem function (e.g., Gibson et al., 2011). In contrast, well-managed shifting cultivation leads to a patchy habitat mosaic of agricultural plots, fallow and forests, and has lower local carbon and biodiversity impacts than more intensive land uses (Gardner et al., 2009). As the cultivation phase is typically short (1-3 years), agricultural plots are often small (less than 1 ha) and close to either primary or older secondary forests that act as recolonisation sources, and soil compaction is limited, biomass and biodiversity can recover rapidly during the fallow phase (Gehring et al., 2005; Lamb et al., 2005).

Uncontrolled human-induced fires, such as those originating from agricultural areas or road edges, can reduce forest biodiversity, particularly in tropical rainforests. For example, large scale fires in Amazonian forests were unlikely to have occurred more than once or twice per millennium (Sanford et al., 1985; Turcq et al.,1998) and the regional flora and fauna shows little adaptation to these episodic disturbance events (Uhl and Kaufmann, 1990; Peres et al., 2003). Fires in the rainforests of Amazonia and Southeast Asia have long-term effects on the composition of the vegetation, with an increase in pioneer species and reduction or loss of mature forest species (Barlow and Peres, 2008; Cochrane and Schulze, 1999; Slik et al., 2002; 2010). A synthesis of Amazonian bird data showed that low-intensity understorey fires can alter species composition more than selective logging, causing avian species changes similar to extreme forest fragmentation (1-10 ha isolated forest fragments; Barlow et al., 2006). Fires also exacerbate the impacts of selective logging and fragmentation on biodiversity, leading to significant reductions of forest-dependent birds and large vertebrate species in fragmented landscapes (Lees and Peres, 2006; Michalski and Peres, 2005).

Unsustainable logging, especially after multiple harvests and where fire is not controlled, can precipitate a shift in forest state, including the loss of a complex canopy, domination by dense undergrowth and pioneer species, loss of important functional species and increases in the abundance of some generalist and *invasive species* (e.g., van Wilgen et al., 2001; Asner et al., 2006; Souza et al., 2005), and a generally impoverished biota (Cleary, 2003). Altered forest states may continue to provide some services but ecosystem functions of degraded secondary tropical forests and their long term successional trajectories is an area of scientific and management uncertainty (Hobbs et al., 2006).

Forests can be degraded through unsustainable hunting that results in loss of game animals for local people and loss or impairment of functional roles provided by these species (Nasi et al., 2008; Harrison, 2011; Thompson et al., in press). Such "empty forests" are common in tropical areas, even where forests are protected (e.g., Redford, 1992; Collins et al., 2011). Vertebrate biomass can drop dramatically from around 700 kg km^{-2} in non-hunted sites to 200 kg km^{-2} in heavily hunted areas in the Amazon (Peres, 2000) and primate relative abundance may decline almost 10-fold in heavily hunted areas of Africa (Oates, 1996), or even go extinct, as was the case for Miss Waldron's red colobus monkey (*Procolobus badius waldroni*), which was endemic in West Africa (Oates et al., 2000). Proper game management is key to maintaining populations. For example, if hunting pressure is not excessive, adjacent undisturbed forests may provide source populations (Siren et al., 2004; Novaro et al., 2000; van Vliet et al., 2010).

Although traditional knowledge sometimes guides sustainable management and use of NTFPs (Parrotta and Trosper, 2012), NTFP harvesting can have significant adverse impacts on forest ecosystems (Belcher and Schrekenberg, 2007). For example, planting and tending the saplings of benzoin trees (*Styrax* spp., tapped for resin) in the understorey of montane forests in Sumatra led, over time, to species-poor tree canopies (García-Fernández et al., 2003), and bamboo production can displace natural forests (Fu and Yang, 2004).

2.5.4 Impacts of deforestation and forest degradation on other ecosystem services

Tropical deforestation leads to complex responses of the biophysical system. Change in land cover from forest to non-forest vegetation increases albedo (i.e., the proportion of solar radiation that is reflected back to the atmosphere). However, deforestation also results in lower evapotranspiration and sensible heat fluxes, resulting in increased surface temperatures and regional reductions in precipitation (Bala et al., 2007; Werth and Avissar, 2004). Deforestation followed by conversion to grassland or cropland, and the associated changes in surface characteristics towards lighter colours, can have a strong impact on changes in albedo. Secondary forest following logging has initially higher dry-season albedo but it declines quickly and within 30 years is indistinguishable from that of the original forest (Giambelluca, 2002). Forest degradation impacts on albedo changes from selective logging may be small if a forest canopy is maintained (Miller et al., 2011). Therefore, the combined impacts of tropical deforestation on the carbon cycle and on biophysical processes (albedo and evapotranspiration) contribute to warming, locally and globally (Henderson-Sellers et al., 1993; Bala et al., 2007; Field et al., 2007). Field et al. (2007) estimated that if the average biophysical forcing from loss of tropical rainforest is 5 watts m^{-2} locally, then the loss of 60 percent of global tropical forest area by 2100 would produce additional warming comparable to an extra 12 Pg C in the atmosphere.

Forests retain moisture from rainfall, allowing recharge of water tables and regulating stream flow. Deforestation and forest degradation typically result in increased soil erosion and sediment loads in streams and rivers, disrupting aquatic systems (Foley et al., 2007). Deterioration of soil fertility, associated with deforestation and degradation pressures, increases the difficulty and cost of restoring forests or growing crops (e.g., Lal, 2005).

Furthermore, the loss of habitats and species can cause dramatic changes in trophic structure and food chains (Wright et al., 2007; Dobson et al., 2006) affecting the provision of ecosystem services mediated by species from different trophic levels; losses from higher trophic levels can trigger a cascade of unexpected effects, such as increased herbivory (Pace et al., 1999; Terborgh and Estes, 2010; Estes et al., 2011). Modifications to trophic interactions can affect key ecosystem functions and services, such as pollination and pest control (Tylianakis et al., 2007), leading to reduced production (including agricultural) and vulnerability to invasion (Laurance et al., 2006; Chapin et al., 2000). A global meta-analysis (Hooper et al., 2012) suggested that loss of plant diversity, especially of key functional species (Diaz and Cabido, 2001), can reduce plant production and decomposition rates (e.g., Cardinale et al., 2011), two key biological processes that influence carbon cycling and provisioning services.

2.5.5 Recovery of forest carbon and biodiversity following deforestation and forest degradation

Recovery of carbon and forest biodiversity following deforestation

The rates of carbon accumulation in above-ground biomass are typically fastest in the first two decades of (sub-) tropical forest succession, although it may take decades for stocks to recover to levels in primary forest (Silver et al., 2000; Feldpausch et al., 2004). Most rapid rates are in tropical rainforests and lowest in dry forests (Silver et al., 2000). Net primary productivity in secondary forests is usually three to five times greater than that of intact forests, but total carbon stocks in secondary forests are lower than in primary forests (Luyssaert et al,. 2008; Lewis et al., 2009). Nevertheless, at a global scale, secondary forests are an important carbon sink that partially compensates for carbon emissions from tropical deforestation (Houghton et al., 2000; Feldpausch et al. 2005; Pan et al., 2011).

Previous land-use practices and their intensity are strong determinants of biomass recovery potential (Fearnside and Guimaraes, 1996; Steininger, 2000). Long periods of intensive use significantly impede vegetation growth (Uhl et al., 1981; Uhl, 1987; d'Oliveira et al., 2011). On a rainforest landscape in Borneo under shifting cultivation for over 200 years, biomass accumulation was significantly lower in sites cultivated six times or more because of a loss in regenerative capacity from seed-banks and of re-sprouting species (Lawrence et al., 2005). Because burning reduces stocks of available nutrients (Holscher et al., 1997; Davidson and Artaxo, 2004), repeated and shorter slash-and-burn cycles can result in progressive nutrient loss and limit capacity for biomass recovery. However, in a former rainforest area of Madagascar, five to seven cropping cycles were found to be sufficient to lead to severe degradation, because of invasion and conversion to exotic grasslands that cannot sustain agriculture (Styger et al., 2007). These results suggest that the time period for damage and recovery varies considerably both within and among forest types.

Along with carbon recovery in tropical secondary forests, a certain proportion of primary forest species is recovered over time (Chazdon et al., 2009; Putz et al., 2012). Forest carbon and biodiversity in tropical secondary forests appear to be positively correlated over the recovery period, at least on a pan-tropical scale, but recovery of biodiversity typically lags behind that of carbon stocks (Guariguata et al., 1997; Chazdon et al., 2009; Gardner et al., 2009; Putz et al., 2012). The retention or management of structurally and floristically complex habitats, like some agroforests, can often ensure the persistence of some forest species in managed landscapes (Chazdon, 2003; Lamb et al., 2005; Scales and Marsden, 2008). Nevertheless, chronosequence studies of regenerating forests demonstrate that biotic recovery occurs over long time scales and that re-establishment of certain species and functional groups can take a century or longer (de Walt et al., 2003; Liebsch et al., 2008). Knowledge gaps remain because of limited long-term data on the recovery of secondary forests across the (sub-)tropics.

Forest structure and composition change continually as a result of disturbances, and natural successional pathways result in shifts in species and their densities over time. However, in highly disturbed forests, the species composition often differs markedly from that expected under natural processes, signifying that the ecosystem state has been altered (Aide et al., 2000; Pascarella et al., 2000). Commonly, fast growing and light-wooded pioneer species that usually only occupy small canopy gaps in primary forests dominate young secondary forests. In highly disturbed landscapes, natural successional processes may be arrested and invasive species, if present in the landscape, may become dominant in the forest canopy (Grau et al., 2003; Lugo, 2002; Chazdon, 2008; Letcher and Chazdon, 2009) resulting in changes in ecological processes, and often the loss of some ecosystem services (e.g., van Wilgen et al., 2001).

Many studies report substantial recovery of biodiversity in secondary forests following slash-and-burn cultivation (e.g., Raman, 2001; Dunn, 2004; Chazdon et al., 2009). The capacity of forests to recover biodiversity during the fallow phase depends, in part, on the duration and intensity of agricultural management. Lawrence (2004) showed a long term erosion of tree diversity resulting from shifting cultivation in Borneo, where the evenness of the tree community declined with each cultivation cycle. A study in rainforests and dry forests in Tanzania comparing the recovery from slash-and-burn agriculture across areas with different fallow periods showed that forest recovery was higher for both biomass and tree diversity after long fallow periods, and recovery occurred only where the cultivation period was less than16 years (Mwampamba and Schwartz, 2011). A review of 65 studies by Dent and Wright (2009) found that secondary forests resulting from low intensity management systems, such as shifting cultivation, appeared to be more similar to primary forests than those regenerating from pastures or intensive agriculture. Nevertheless, caution is needed in interpreting these latter results because few taxa were studied, and they often lacked proper spatial coverage, sufficient replication or appropriate controls (Gardner et al., 2007; Lewis, 2009)

Recovery of carbon and forest biodiversity after forest degradation

The consequences and recovery times for forest carbon depend on the level, scale and forms of degradation. In some cases, recovery from degraded alternative stable states is not possible without substantial management (e.g., van Wilgen et al., 2001). Repeated burning has a strong detrimental effect on carbon accumulation in secondary forests, with five or more burnings reducing total carbon accumulation by over 50 percent (Zarin et al., 2005). In areas subject to excessive burning, secondary forests are unable to recover their original biomass within the average fire-return interval for several reasons: continuing post-fire mortality (Baker et al., 2008; Barlow et al., 2003; 2010), reduced carbon accumulation rates with repeated fires (Zarin et al., 2005) and changes in species composition in burned forests towards short- lived, fast-growing species with low wood density (Barlow and Peres, 2008; Cochrane and Schulze, 1999; Slik et al., 2010; Slik et al., 2002).

Some forest species recover slowly over time after fire. For example, the avian species composition of burned forests can become less similar to that found in unburned forests over time due to lag-effects in biodiversity responses (Adeney et al., 2006; Barlow and Peres, 2004). Shifts in species composition following timber extraction can either be temporary (e.g. bats in Trinidad; Clarke et al., 2005) or persist for decades or more (e.g., ants in Sri Lanka; Gunawardene et al., 2010 or plants in India; Devi and Behera, 2003). Ecosystem recovery following logging also depends on the methods used (Asner et al., 2004), and differences in the condition of the forest prior to logging can have a dramatic impact on trajectories of ecological recovery. Bischoff et al. (2005), working in Borneo, found that logging late successional forest characterised by dense understorey pioneer vegetation, after disturbance over 100 years ago, resulted in an increase in shade-tolerant and small stature tree species at the expense of canopy hardwood species. There is some indication of greater levels of biotic resilience to logging in forests that are regularly exposed to natural disturbances (e.g. fire and hurricanes in Belize; Whitman et al., 1998) or regions that underwent a relatively rapid expansion and contraction of forest areas during the Pleistocene (e.g. West Africa; Ernst et al., 2006). A lack of long-term data on the recovery of secondary forests across the (sub-) tropics means that the time required to recover the forest biota to a desirable state remains highly uncertain.

The emergence of novel (sub-)tropical forests

Accumulating human impacts with consequent cascading effects on biological processes and unpredictable stochastic effects combine to generate ecological conditions and species interactions that have no evolutionary precedents (e.g., Tylianakis, 2009). These degraded forests and recovering deforested areas have resulted in novel ecosystems globally (e.g., van Wilgen et al., 2001; Hobbs et al., 2006; Lindenmayer et al., 2008). Such new species assemblages may or may not provide all of the goods and services that humans need because often original dominant functional species have been lost or reduced in numbers, with the commensurate alteration of processes (e.g., Olden et al., 2004; Lewis, 2009).

There is growing evidence to suggest that the rate of many ecological processes may be both magnified and accelerated in modified tropical forest landscapes, with unpredictable implications for the maintenance of biodiversity (Lewis, 2009; Laurance et al., 2002). Novel systems may foster new patterns of species loss as extinction is most likely to occur when new threats or combinations of threats emerge that are outside the evolutionary experience of species, or threats occur at a rate that outpaces adaptation (Brook et al., 2008). However, novel systems can also provide important refuges for recovering forest biodiversity in areas that have been reforested or highly degraded. For example, in Puerto Rico, the naturalisation of introduced tree species on abandoned agricultural lands is thought to have played an important role in the recovery of many native species (Lugo and Helmer, 2004).

Although the definition of what constitutes a ‘novel ecosystem’ remains somewhat arbitrary, their emergence follows the selective loss and gain of key taxa, the creation of dispersal and regeneration barriers, or changes in system productivity that fundamentally alters the relative abundance and structure of resident biota (Hobbs et al., 2006). Two compelling examples are the creation of ‘new forests’ in Puerto Rico that are comprised of species assemblages that have not previously been recorded (Lugo and Helmer, 2004), and the major alteration of the structure of native Hawaiian rainforests following the naturalisation of numerous alien invasive plants (Asner et al., 2008).

Understanding the structure and function of novel ecosystems is of fundamental importance in evaluating patterns of biodiversity change, and the potential for biodiversity recovery in degraded areas (Chazdon, 2008).

2.6 Conclusions

1. Biodiversity maintains critical ecosystem processes (e.g., seed dispersal, photosynthesis) and underpins the provision of many forest ecosystem services. For some ecosystem services, such as pollination, there is a direct link between species richness and the provision of the service. Other ecosystem services, such as erosion control, are largely independent of species composition and richness. Larger areas of forest are essential for the provision of many ecosystem services (e.g. carbon storage, climate regulation), are more productive and deliver mores services than small forest patches because of higher biodiversity, reduced edge effects and less human access. Small forest patches do maintain some services in highly modified landscapes.

2. Forests contain most of Earth's terrestrial biodiversity, especially in (sub-)tropical rainforest, moist forest and montane systems. Deforestation and forest degradation within these ecological zones are the largest drivers of terrestrial biodiversity decline.

3. Very extensive areas of degraded forests and of deforested areas now exist in tropical and sub-tropical regions, with significant adverse effects on conservation of carbon stocks and biodiversity, and thus on the provision of many ecosystem services. The combined impacts of past and ongoing degradation on forest carbon and biodiversity may approach those of deforestation.

4. Ecosystems can exist in various states, but not all states provide the same level of ecosystem services. Human-induced losses of biological diversity can adversely affect the resilience of forest ecosystems, and hence the long-term provision of services. To avoid catastrophic change, managers need to ensure that ecosystems remain within a 'safe operating space'.

5. In forests with few tree species such as most planted forests, increases in tree species richness may lead to increased biomass carbon stocks and some other services under appropriate conditions. At high levels of diversity, the relationships between changes in species richness and production remain poorly understood.

6. Different forest types and ages can vary markedly in levels of biodiversity and the amount of carbon stored in different pools; however primary forests store high levels, while young forests sequester carbon rapidly. Accordingly land use planning processes need to take these differences into account when addressing both biodiversity and carbon objectives.

7. In (sub-)tropical forests recovering from major disturbance, carbon and biodiversity both increase over time, but recovery rates for both diminish over time, and recovery of biodiversity is typically much slower than that of carbon.

8. Due to the large number of endemic species, endangered species, and unique species assemblages in (sub-)tropical forests, spatial planning for biodiversity conservation objectives needs to be more area specific than is necessary for carbon management.

9. There is uncertainty with respect to the capacity of 'novel' forest ecosystems, which differ in composition and/or function from past systems as a consequence of changing species distributions and environmental alteration, to provide expected goods and services in future.

Significant gaps exist in our understanding of the relationships between biodiversity and ecosystem functioning and provision of forest ecosystem services, including carbon sequestration, and how these relationships are affected by forest condition.

- The majority of scientific studies have not distinguished the effects of species composition on forest productivity and other ecosystem functions, from the effects of either species richness or of individual species. Further work is needed to better understand: (i) the relationships between plant species richness and functional diversity, and biomass accumulation in diverse forest systems, especially for novel systems; (ii) the relationships between species richness and ecosystem resistance (to chronic disturbances); (iii) the cascading effects of the loss on faunal diversity on forest ecosystem processes; (iv) the long-term effects of repeated degradation events on rates of recovery of forest ecosystems; (v) the existence of degradation/disturbance thresholds or tipping points beyond which recovery of expected biodiversity, ecosystem functions and provision of services is severely constrained.

- Further work is needed to improve our knowledge of the magnitude and dynamics of below-ground carbon stocks and fluxes in different forest types. The time scales and conditions required to recover to pre-disturbance levels of biodiversity and carbon in secondary forests (which are of significant value to conservation of both carbon and biodiversity), are poorly understood. There is also considerable uncertainty regarding the levels of ecosystem service provision from increasingly widespread novel ecosystems that result from prolonged anthropogenic impacts.

Annex 2.1

Selected studies in all types of forests on the relationship between species richness and carbon fluxes and storage

Ecological Zone	Location	Forest Stand Type	No. Tree Species	Age (y)	Carbon pools	Carbon Fluxes	Type of relationship Biodiversity vs Carbon	Positive (+) Negative (-) Neutral (0)	Reference
Sub-tropical moist	Puerto Rico	Planted (experimental)	1 to 4	8.5	Soil; above-ground biomass	Net Primary Production (NPP), decomposition	Carbon increase in mixed species plantations	+	Parrotta (1999)
Sub-tropical rainforest	Costa Rica	Planted (experimental)	1, 8	5	Above-ground biomass	NPP	Biomass greater in mixed plantations than in monocultures	+	Montagnini (2000)
Sub-tropical	Costa Rica	Planted (experimental)	1 to 3	13	Above-ground biomass	NPP	Higher growth rates in mixed plantations	+	Petit and Montagnini (2004)
Sub-tropical rainforest	Puerto Rico	Natural	50+	multi	Above-ground biomass	NPP	Positive relationship between biodiversity and AGB but varied in strength with the indicator and age of stand.	+	Vance-Chalcraft et al. (2010)
Tropical humid	Australia	Planted (commercial)	1 to 8		Above-ground biomass	NPP	Higher tree growth rates with increase sp. richness	+	Erskine et al. (2006)
Tropical rainforest	Australia	Planted (commercial)	1 vs. 2	10	Above-ground biomass	NPP	Two species resulted in superior growth rates than either species alone.	+	Bristow et al. (2006)
Tropical rainforest	Panama	Planted (experimental)	6	6	Litter	Litter decomposition	Significant effects of tree species richness on total litter production; litter decomposition not affected by tree species richness	+	Scherer-Lorenzen et al. (2007)
Tropical rainforest	Australia	Planted (experimental) & Natural	2 to multi	23-72	Above-ground biomass	NPP	No relationship between diversity and production in old forests (ie, possible age effect)	0	Firn et al. (2007)
Tropical rainforest	Panama	Natural	multi		Above-ground biomass	NPP	No relationship between tree-species diversity and above-ground carbon stocks	0	Kirby and Potvin (2007)
Tropical rainforest	Panama	Planted (experimental)	1 vs 2 (total 6)	3	Above-ground biomass	NPP	Tree biomass higher in pairs and plots with higher species richness	+	Murphy et al. (2008)
Tropical rainforest	Panama	Planted (experimental)	1 vs 2 (total 6)	3	Belowground biomass		No significant differences in root or microbial biomass	0	Murphy et al. (2008)
Tropical rainforest	Panama	Planted (experimental)	1 vs 2 (total 6)	3	Soil	Soil respiration	Soil respiration 19–31% higher in monoculture than in pairs and plots with higher species richness	-	Murphy et al. (2008)
Various (Review)	Tropics	Planted (experimental)	2 -4	1.5-14	Above-ground biomass	NPP	Mixed plantations had higher diameter growth rate	+	Piotto (2008)
Tropical rainforest	Panama	Planted (experimental)	1,3,6	4,5	Above-ground biomass	NPP	Species diversity explained 23% of productivity and 30% of mortality	+	Healy et al. (2008)
Tropical rainforest	Borneo	Natural			Soil		Tree diversity negatively correlated with organic carbon content	-	Slik et al. (2009)

Tropical rainforest	Brazil	Planted (experimental)	2, 4 or 7		Litter	Litter decomposition	Species composition, but not species richness, significantly influenced litter decomposition rates	0	Giesselmann et al. (2010)
Tropical rainforest	Panama	Natural	30-61	~200	Above-ground biomass		Species richness increases tree carbon storage	+	Ruiz-Jaen and Potvin (2010)
Tropical rainforest	French Guyana	Planted (experimental)	16		Litter	Litter decomposition	Effects on decomposition mostly driven by species composition; functional litter diversity in chemical traits did not explain decomposition	0	Barantal et al. (2011)
Tropical rainforest	Panama	Planted (experimental)	6	8	Litter; Soil	CWD decomposition Litter decomposition; Soil respiration	Significant effects of diversity on CWD decomposition and soil respiration	+	Potvin. et al. (2011)
Tropical rainforest	Panama	Planted (experimental)	6	8	Soil Below-ground biomass		No diversity effects on the carbon pools No significant differences in root or microbial biomass	0	Potvin. et al. (2011)
Tropical rainforest	Panama	Planted (experimental) & Natural	6		Above-ground biomass		Tree carbon storage in the mixed-species plantation was mainly explained by species richness and in the natural forests by functional trait diversity	+	Ruiz-Jaen and Potvin (2011)
Temperate	Southwest China	Natural	48, 80, 143 & 310		Above-ground biomass		No relationship species richness and above-ground carbon; significant negative relationship between species diversity and above-ground carbon storage	0 -	Zhang et al. (2011)
Boreal	Sweden	Natural			Above- and below-ground biomass		Vascular plant richness and diversity was positively correlated to total carbon storage; negatively correlated with above-ground C storage; positively correlated to below-ground carbon storage	+	Wardle et al. (2012)
Temperate and tropical	Global	Model, Natural			Above-ground biomass	NPP	No relationship at very large scales between tree species richness and biomass/ha	-	Enquist and Niklas (2001)
Temperate	USA	Survey data			Above-ground biomass	NPP	Positive relationship between tree biomass and species richness across USA	+	Caspersen and Pacala (2001)
Temperate	Germany	Planted (experimental)			Above-ground biomass	NPP	Positive relationship between species richness and tree biomass	+	Pretzsch (2005)
Temperate	UK	Planted (experimental)			Above-ground biomass	NPP	Positive relationship between species richness and tree biomass	+	Jones et al. (2005)
Temperate & Boreal	Canada	Planted (experimental) & Natural	1 to 13		Above-ground biomass	NPP	Positive relationship in temperate forests and in boreal forests	+	Paquette and Messier (2011)

Annex
2.2

Forest area and above-ground biomass (AGB) carbon and total biomass carbon by region and ecological zone in the tropical and sub-tropical domain. Based on the Saatchi et al. (2011) tropical biomass maps*, the FAO ecological zones (Figure 1.1; FAO, 2001) and the MODIS forest cover map (25 percent forest cover threshold) (NASA, 2010). Carbon is defined as 50 percent biomass. SD is standard deviation of spatial variations of the estimates across the regions; SE represents standard errors of the estimates, i.e. uncertainties associated with all errors from data sources and estimation methods

Region	Forest Area (Mha)	AGB carbon density (Mg C ha^{-1})		Total biomass carbon density (Mg C ha^{-1})	
		Mean ± SD	SE (±)	Mean ± SD	SE (±)
Africa					
Tropical rainforest	252.9	107 ±51	37	135 ±64	47
Tropical moist deciduous forest	110.6	38 ±18	13	50 ±23	17
Tropical shrubland	1.6	41 ±25	14	53 ±32	17
Tropical dry forest	36.1	38 ±18	13	49 ±23	16
Tropical mountain system	22.7	64 ±39	22	82 ±49	28
Sub-tropical humid forest	1.5	38 ±15	13	49 ±19	17
Sub-tropical dry forest	0.7	31 ±16	11	41 ±21	14
Sub-tropical mountain system	1.1	34 ±11	11	45 ±14	15
Africa Total	**427.2**	**80 ±78**	**27**	**102 ±98**	**35**
Latin America					
Tropical rainforest	587.1	115 ±34	37	146 ±42	47
Tropical moist deciduous forest	179.3	54 ±42	18	69 ±53	24
Tropical shrubland	0.9	55 ±41	19	71 ±51	24
Tropical dry forest	47.6	27 ±23	10	36 ±29	13
Tropical mountain system	71.8	86 ±50	29	110 ±62	37
Sub-tropical humid forest	20.4	51 ±38	18	66 ±48	23
Sub-tropical dry forest	5.3	55 ±51	20	71 ±64	25
Sub-tropical mountain system	7.2	21 ±23	8	27 ±29	10
Latin American Total	**919.8**	**94 ±110**	**31**	**119 ±138**	**39**
Southeast Asia					
Tropical rainforest	261.6	121 ±50	44	153 ±62	56
Tropical moist deciduous forest	55.6	105 ±49	37	133 ±61	47
Tropical shrubland	2.5	64 ±39	23	82 ±49	29
Tropical dry forest	17.6	83 ±50	30	106 ±63	38
Tropical mountain system	53.6	128 ±34	43	162 ±42	55
Sub-tropical humid forest	0.8	88 ±34	32	112 ±42	41
Sub-tropical mountain system	7.7	101 ±41	37	128 ±52	47
Southeast Asia Total	**399.5**	**118 ±114**	**42**	**149 ±142**	**54**
All Total	**1,746.5**	**96 ±177**	**32**	**122 ±221**	**41**

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* AGB was mapped using a combination of data from in-situ inventory plots and satellite light detection and ranging (LIDAR) samples of forest structure, plus optical and microwave imagery. Below-ground biomass (BGB) was calculated as a function of AGB (BGB = 0.489 AGB0.89) with total biomass = AGB+BGB (for more information see Saatchi et al., 2011)

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