Chapter 6
Carbon fluxes and storage in forests and landscapes

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Abstract We begin this chapter with a discussion of the major carbon fluxes (e.g., gross primary production, ecosystem respiration) and stocks (e.g., aboveground biomass) in forest ecosystems, as well as their relationships, and provide examples of their values from selected case studies. We pay special attention to the magnitudes of these fluxes and stocks in different forests and biomes. However, studies of carbon cycling at a landscape scale lag significantly behind those at an ecosystem level. The objective of this chapter is to provide a glimpse of current knowledge of carbon fluxes and storage in forests at both ecosystem and landscape scales. Due to the overwhelming literature on this topic, we have limited our review to lessons from selected empirical studies that demonstrate the temporal and spatial variations of the carbon cycle in a range of representative environments We further discuss our current understanding of carbon cycles across forests and landscapes in the contexts of climate change, the impact of natural disturbances, and regulation of the carbon cycle by management actions. We present a new conceptual framework for the changes in net ecosystem production following a disturbance as a foundation

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to guide future studies. Finally, we share our vision of the direction of future carbon cycle research from both basic and applied perspectives. We support our review by citing relevant papers that provide important references for readers

6.1 Introduction

Ecosystem play a major role in the global carbon cycle, as they store 45 % of the terrestrial carbon and account for ~50 % of soil carbon sequestration (Bonan 2008) A recent report based on long-term global inventory data indicated that the total forest carbon sink since 2000 amounts to 22 % of the global carbon sink, and that this sink is offsetting 33 % of current annual fossil fuel emissions (Pan et al. 2011). However, both carbon fluxes and storage in forests vary significantly over time (e.g., annual, decadal) and space (regional, global), and both are directly regulated by natural events (e g., climate change, drought, wildfires, pest or disease outbreaks) and human activities (e.g., deforestation, plantation establishment, urban sprawl, management practices). For example, tropical deforestation is responsible for the release of about 1 5 Gt C per year, accounting for ~15 % of total anthropogenic carbon emissions (Peters et al. 2011). As the international community begins to address the impacts of global climate change through the development of adaptation plans (IPCC 2007), a thorough understanding of the forest carbon cycle as well as the mechanisms that regulate coupled human and natural stressors becomes increasingly important for both the scientific community and the decisionmaking community (Baccini et al. 2012, Birdsey et al. 1993, Davidson et al. 2012).

Scientific investigations of forest carbon cycling during the past three decades have been conducted using different representations of carbon storage that were based on societal needs. Prior to the 1980s, the carbon cycle was mostly investigated from the perspectives of timber yield and ecosystem production In the 1980s, forests were hypothesized to be responsible for the missing carbon needed to close the global carbon budget, and some researchers believed that the ability of forests to sequester carbon had been significantly underestimated.

When ecosystem management emerged as the new paradigm in natural resource management in the early 1990s, researchers took advantage of the rapid advances in technology (e.g., remote sensing, eddy-covariance flux towers, stable-isotope analysis) and of new generations of ecosystem models to seek answers for questions such as the following What determines the carbon sink strength of forest ecosystems under alternative forms of management? Can increased carbon sequestration be achieved through more intensive management? What is the relative importance of climate and disturbance in affecting the mean carbon flux and its variation? How do different fragmentation patterns affect landscape-scale carbon fluxes? Through the promotion of data sharing among research labs across the globe, the scientific community has made significant progress in understanding how forests differ in their carbon fluxes and stocks. This collective effort using open data sources has led to increasing studies of the carbon cycle at regional, continental, and global scales

(e g , John et al. 2013, Turner et al 1995, Xiao et al 2009, 2010, 2011, Yi et al 2010; Zhang et al 2012).

Recently, pressing issues arising from the high demand for renewable energy (e g., fast-growing crops such as poplar (*Populus* spp) and eucalyptus (*Eucalyptus* spp) plantations to produce cellulosic ethanol) and the CO_2 emission-reduction targets adopted by many countries (e g., IPCC 2007) triggered a new dimension in carbon cycle science (e.g., life-cycle assessment of the carbon cycle; Gelfand et al. 2011), emphasizing carbon's role in global warming (Robertson et al 2008) and linking the carbon cycle with socioeconomic systems (e.g., carbon stocks, urbanization; Peters et al 2011) In addition, the increasing magnitude and frequency of natural disturbances and extreme climatic events challenge our in-depth understanding of their roles in regulating carbon fluxes and stocks (e.g , Davidson et al. 2012, Gu et al 2008) However, the core ecological research on this topic focuses on understanding the magnitude of carbon fluxes and stocks and identifying the underlying mechanisms responsible for changes in these factors in time and in space.

6.2 Carbon cycling in forests

Carbon enters a forest from the atmosphere, mostly through photosynthesis, and its storage in the forest is commonly known as "gross primary production" (GPP) or "carbon assimilation". A small amount is also input from the weathering of bedrock (M_c) and by lateral transfer by animals (A_c) and by the wind (W_c). GPP is simultaneously used to create biomass and to maintain plant metabolism through autotrophic respiration (R_A) of live tissues (e.g., leaves, stems, and roots). R_A can be broadly separated into aboveground and belowground respiration (i.e , R_{Aa} and R_{Ab}, respectively, Hanson et al. 2000). Net primary production (NPP) equals the difference between R_A and GPP, and can be divided into aboveground (ANPP) and belowground (BNPP) components. The remaining portion of GPP (i.e., NPP) can be divided into aboveground carbon allocation (AGCA) and belowground carbon allocation (BGCA), which serve as a food source for animals (A_c) and as a substrate for decomposition by decomposer organisms (D) into various trace gases (e.g., CO_2, CH_4) before returning to the atmosphere Emissions from A_c and D are termed "heterotrophic respiration" (R_H). Forests include both live and dead organic matter (e g., snags, dead branches, leaves), suggesting that a small amount of aboveground heterotrophic respiration (R_{Ha}) exists This is especially true for the tropical and subtropical rainforests, where epiphytes are abundant for elevated decomposition of aboveground dead organic matter due to the high temperature (Clark et al 2001) The sum of R_A and R_H is the total respiratory loss of a forest and is referred to as ecosystem respiration (R_e). The total amount of carbon loss from the soils—the sum of belowground autotrophic respiration (R_{Ab}) and belowground heterotrophic respiration (R_{Hb})—is termed "soil respiration" (R_s; Curtis et al 2005, Hanson et al. 2000, Li et al. 2012) Most forests are on slopes and, therefore, the lateral fluxes of carbon

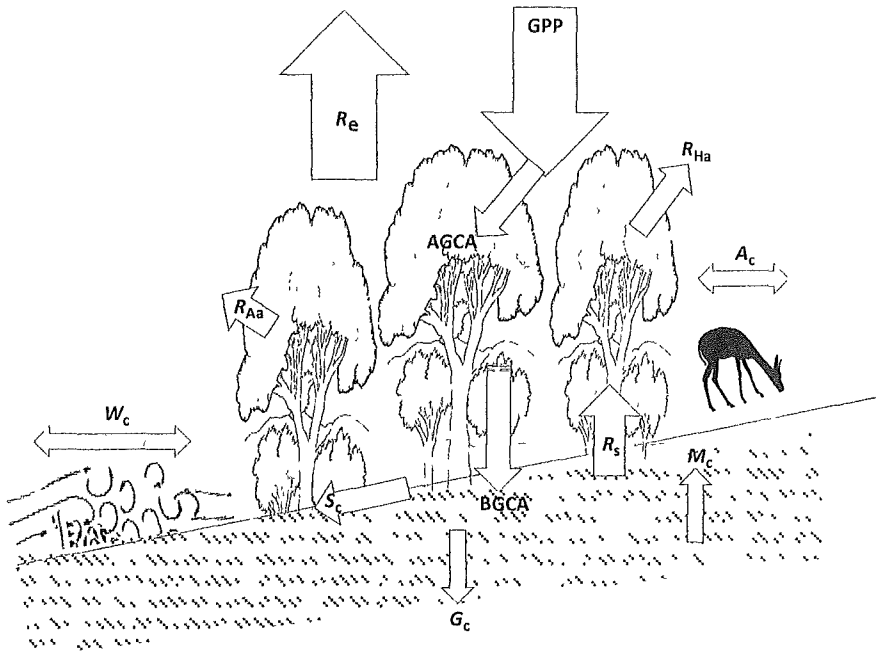

Figure 6.1 Illustration of the major carbon fluxes in a forest ecosystem, including gross primary production (GPP), ecosystem respiration (R_e), aboveground carbon allocation (AGCA), belowground carbon allocation (BGCA), soil respiration (R_s), aboveground heterotrophic respiration (R_{Ha}), aboveground autotrophic respiration (R_{Aa}), surface runoff (S_c), lateral fluxes of carbon through the wind (W_c) and animals (A_c), vertical water leaching (G_c), and upward movement through diffusion after weathering of bedrock (M_c) in the soil

through the wind (T_c, such as fine litter, leaves) and of organic materials through animals (A_c) may be significant. Finally, surface runoff (S_c) and vertical water leaching (G_c) will carry small amounts of carbon into or out of a forest (Fig. 6.1). These carbon fluxes and their relationships can be summarized as follows:

$$\text{GPP} = [\text{NEP} + R_e]$$
$$\text{NPP} = [\text{GPP} - R_A]$$
$$\text{NPP} = [\text{ANPP} + \text{BNPP}]$$
$$\text{ANPP} = \text{Vegetation Growth} - \text{Litterfall}$$
$$\text{BNPP} = \text{Root Growth} - \text{Root Mortality}$$
$$R_e = [R_A + R_H] - (M_c)$$
$$R_A = R_{Aa} + R_{Ab}$$
$$R_H = [R_{Ha} + R_{Hb}] - (M_c)$$
$$\text{NEP} = [\text{AGCA} + \text{BGCA}] + (S_c + T_c + G_c + A_c - M_c)$$
$$R_s = [R_{Ab} + R_{Hb}] - (M_c)$$

where NEP represents net ecosystem production, the flux terms inside the square brackets account for large proportions of the total, and those inside the round brackets are minor or difficult to quantify.

The magnitudes of these flux terms vary significantly among ecosystems and over time. Among them, GPP and R_e are the two largest fluxes, and the difference between them determines the carbon sequestration strength of an ecosystem (Chen et al. 2004, Schwalm et al. 2010). For example, Yuan et al. (2009) found that GPP explained a significant proportion of the spatial variation of NEP across evergreen needleleaf forests (also see Luyssaert et al. 2007). Conversely, R_e determines the magnitude of NEP for a range of deciduous broadleaf forests (Yuan et al. 2009). The global average GPP of forests is approximately 880 g C m^{-2} yr^{-1}, but varies from less than 500 g C m^{-2} yr^{-1} to nearly 3000 g C m^{-2} yr^{-1}, with the highest values in the humid tropics (e.g., Amazonia, central Africa, southeast Asia), where both temperature and moisture requirements are satisfied for photosynthesis (Sun et al. 2011, Yuan et al. 2010). Extremely high GPP has also been reported in plantations of loblolly pine (*Pinus taeda*; >2300 g C m^{-2} yr^{-1}; Gough et al. 2002, Noormets et al. 2012) and eucalyptus in Brazil (*Eucalyptus* spp.; 6640 g C m^{-2} yr^{-1}; Stape et al. 2008). The deciduous forests at high latitudes (e.g., the boreal region) have lower GPP levels, at 460 g C m^{-2} yr^{-1} or lower (Li et al. 2007a). The growing season length, annual precipitation, and temperature are the three most critical variables that determine GPP and its changes over time. Recent studies have shown that extended droughts (Xiao et al. 2009) and disturbances (Amiro et al. 2010) can substantially reduce NEP, primarily by reducing GPP while simultaneously altering R_e.

For forests that are carbon sinks, R_e is slightly smaller than GPP but of similar magnitude and varies from 300 to 600 g C m^{-2} yr^{-1} in boreal forests, from 600 to 900 g C m^{-2} yr^{-1} in temperate forests, and from 1000 to 2500 g C m^{-2} yr^{-1} in tropical forests (Yuan et al. 2010). The global average R_e is approximately 790 g C m^{-2} yr^{-1}, with the highest values occurring in the tropical moist forests and lowest values in the cold tundra and dry desert regions. Luo and Zhou (2006) also reported that the tropical moist forests have significantly higher R_e than other ecosystems, which results in mean NEP values of 400, 275, and 120 g C m^{-2} yr^{-1} for the tropical, temperate, and boreal forest biomes, respectively (Bonan 2008). In forest plantations, NEP can exceed 1000 g C m^{-2} yr^{-1}, making them good candidates for bioenergy systems for ethanol production (e.g., from eucalyptus or poplar). Consequently, alternative management practices are often sought to increase GPP or decrease R_e because forest NEP is determined by their balance. For recently disturbed or old-growth forests that release carbon into the atmosphere, R_e is typically larger than GPP.

For many forests, the amount of carbon emitted by forest soils as R_{Ab} and R_{Hb} (i.e., as R_s) accounts for the majority of R_e (60 to 80 %). R_s depends strongly on soil temperature, soil moisture, and total soil organic matter, which are important regulators of the metabolic processes involved in belowground R_{Ab} and R_{Hb} (Edwards and Sollins 1973, Martin et al. 2009). Consequently, soil temperature and moisture are often used to calculate R_s using simple temperature-based exponential models or other model forms such as the Lloyd and Taylor or Boltzmann–Arrhenius models (Davidson et al. 2005, Li et al. 2012; Noormets et al. 2008, Perkins et al. 2011, Reichstein et al. 2005; Richardson et al. 2006, 2007). Interestingly, the regulation of R_s by thermal and moisture conditions is not linear, instead, optimal and threshold

values exist (Niu et al 2012, Xu et al 2011) In recent years, the scientific community has recognized that both phenology and GPP can directly affect R_{Ab} (DeForest et al. 2006, Hogberg et al 2001) Currently, we lack reliable methods to partition R_{Ab} and R_{Hb}, preventing us from estimating the magnitudes and dynamics of these two terms For managers who are interested in increasing carbon sequestration (i e , increasing the sink strength), soil seems to be the only place to store carbon in the long term because trees and understory vegetation will ultimately die and then decompose, releasing CO_2 back into the atmosphere (Noormets et al. 2012) Consequently, researchers who study the carbon cycle have focused on R_s (Euskirchen et al. 2003, Noormets et al. 2008, Xu et al 2011)

Other carbon flux terms are typically small and have received significantly less attention despite their importance in some forests For example, few studies have examined the amount of carbon lost through runoff and groundwater that will eventually leave the forests through streams and rivers (Bolin et al 1979; Cardille et al 2007, Hope et al. 1993, 1997; Roulet and Moore 2006) Richey et al (2002) found that outgassing ("evasion") of CO_2 from the rivers and wetlands of the central Amazon basin constitutes an important carbon loss process, equal to 1.2 Mg C ha^{-1} yr^{-1}, which is equivalent to more than 30 % of forest NEP in the region Two major studies on the efflux of CO_2 released from inland rivers and streams in the United States found that they were supersaturated with carbon and emitting 97 ± 32 Tg C yr^{-1} (Butman and Raymond 2011, Melack 2011). Nevertheless, the loss of carbon in most of the world's watersheds remains unknown. In addition, carbon fluxes associated with horizontal movements by wind and wildlife that directly carry carbon into or out of a forest have not been studied in the context of the complete carbon cycle.

The magnitudes of all of the components of the carbon cycle are not static, but vary greatly over time. Although pronounced seasonal changes are coupled well with interannual climatic variations, mounting evidence suggests that the variations over periods of two or more years (i.e., an interannual scale) or even at decadal scales are significant (Gough et al. 2008b, Richardson et al. 2007). For example, at the Oak Openings forest in northwestern Ohio, we found higher-than-average NEP, with values that varied from 1.9 to 4.1 Mg C ha^{-1} yr^{-1}, likely due to a combination of climatic variation, drought, and disturbances such as fires (Noormets et al 2008). In a maple (*Acer* spp.) forest in Japan, Saigusa et al. (2005) estimated the annual NEP to be 237 ± 92 g C m^{-2} $year^{-1}$ (mean ± SD) from 1994 to 2002, but NEP varied from 59 to 346 g C m^{-2} yr^{-1} between years (i.e , an interannual variability of up to 287 g C m^{-2}). In the Pacific Northwest of North America, Krishnan et al. (2009) found that a 57-year-old Douglas-fir (*Pseudotsuga menziesii*) stand was a moderate carbon sink, with annual NEP ranging from 267 to 410 g C m^{-2} yr^{-1} during a 9-year period This variation was much higher than that in an old-growth forest in southern Washington State, which was generally a weak carbon sink and could occasionally become a carbon source (Chen et al. 2004).

The cumulative NEP is the amount of carbon stored in a forest without physical removal of carbon from the ecosystem by disturbances such as timber harvesting, commercial thinning, or wildfire (i.e., carbon storage = $\sum$[NEP − removals]).

Forests store a large amount of carbon, with 471 Pg C (55 % of total forest carbon) in tropical forests, 272 Pg C in boreal forests, and 119 Pg C in temperate forests (Pan et al 2011) This totals an estimated 862 Pg C, with 44 % in the soils, 42 % in live biomass, and 8 % in deadwood However, these proportions vary greatly among ecosystem types, climates, disturbance histories, land-use histories, management types, and soils (McKinley et al 2011). Globally, tropical forests stored 56 and 32 % of carbon in their biomass and soil, respectively, whereas boreal forests store 20 and 60 % of the carbon in the biomass and soil, respectively (Pan et al. 2011). In the United States, McKinley et al. (2011) reported that the forests contained ~41 000 Tg C and that this storage increased at a rate of 192 Tg C yr^{-1}

The major carbon pools in forests include living overstory and understory vegetation, dead biomass (e g , coarse woody debris, snags, litterfall, dead roots), and soils The amount of carbon stored in animals is small in most ecosystems and has rarely been studied or considered in the context of a forest's carbon budget. However, this distribution varies greatly among forests and regions A few selected sites from the literature have total carbon storage (excluding animal biomass) ranging from less than 100 Mg C ha^{-1} to as high as 700 Mg C ha^{-1}, but most values are between 200 and 450 Mg C ha^{-1} (Table 6.1) On average, mineral soils contain the largest carbon pools in the national and north-central regions of the United States, where they account for approximately 42 and 52 % of total forest carbon, respectively (Turner et al. 1995). In contrast, live trees represented the largest carbon pool in the Missouri Ozarks and the Pacific Northwest, respectively, accounting for about 55 and 71 % of total forest carbon (Li et al 2007b). The carbon pools of a mixed oak (*Quercus* spp) forest in the southeastern Missouri Ozarks contain 182 Mg C ha^{-1} (Li et al 2007a), with 80 2 Mg C ha^{-1} in living trees, 22 9 Mg C ha^{-1} in dead biomass, 20 0 Mg C ha^{-1} in roots, and 53.7 Mg C ha^{-1} in the soil (i.e., total soil carbon except roots). The mean live tree carbon pool at the site was ~17 and 21 % higher than the national average and the average for the north-central United States, respectively (Turner et al 1995), but it was 16 % lower than the average for the Pacific Northwest (Smithwick et al. 2002). The mean soil carbon was about 16 % higher than that in the Pacific Northwest (Smithwick et al. 2002), but was 12 and 22 % lower than averages for the nation and for the north-central United States, respectively (Turner et al 1995). On average, these results suggest that temperate forests store approximately 50 % of their carbon as aboveground biomass (AGB) and 50 % as belowground biomass (BGB) However, this estimate is imprecise because carbon pool estimates are influenced differently by site-specific disturbance regimes and because the definitions of some major carbon pools (especially for dead organic matter) vary significantly among studies (Bradford et al 2008, Grier and Logan 1977, Matthews 1997, Schlesinger 1997).

The carbon storage in global forests varies greatly in both its magnitude and its within-system distribution (Table 6 1). Overall, tropical forests have high AGB but not necessarily high BGB (e.g , 305 Mg ha^{-1} AGB but negligible BGB for the Tapajos National Forest in the east-central Amazon, Saner et al 2012) Keith et al (2009) claimed that *Eucalyptus regnans* forests in Victoria, Australia, have the highest biomass in the world In contrast, the BOREAL study found that up to 88 % of

Table 6.1. Carbon storage as aboveground biomass (AGB), belowground biomass (BGB), and coarse woody debris (CWD), and the total of these three components, in selected representative forests from the three dominant forest biomes

Biome	Region	Dominant species	Carbon storage (Mg C ha^{-1})				Source
			AGB	BGB	CWD	Total	
Tropical	Tapajos National Forest	*Sclerobium chrysophyllum*	305.00	NA	NA	339.2	Nepstad et al. (2002)
	Sabah, Borneo	*Shorea* spp.	128.00	NA	70.60	210 75	Saner et al (2012)
Temperate	WRCCRF, WA, USA	*Pseudotsuga menzesii*	313.23	174.22	NA	487 45	Harmon et al (2004)
	MOFEP, MO, USA	*Quercus* spp.	80.20	73 70	22.90	182.7	Li et al. (2007b)
	Walker Branch, TN, USA	*Quercus* spp. *Acer* spp.	97.30	91 90	NA	189.20	Curtis et al (2002)
	MMSF, IN, USA	*Acer saccharum* *Quercus* spp	101.90	124.30	NA	226 20	Curtis et al (2002)
	Harvard Forest, MA, USA	*Quercus* spp	105 00	111.60	NA	216.60	Curtis et al (2002)
	UMBS, MI, USA	*Populus* spp.	62.60	NA	NA	78.60	Curtis et al (2002)
	Willow Creek, WI, USA	*Populus* spp. and *Acer* spp	78.60	222 70	NA	301.03	Curtis et al (2002)
	Victoria, Australia	*Eucalyptus regnans*	1819.0	1025.0	NA	2844 0	Keith et al (2009)
	Chiloé Island, Chile	*Nothofagus nitida*	290.50	NA	158.00	448.50	Carmona et al (2002)
Boreal	Saskatchewan, Canada	*Populus* spp	93.34	35.99	291.10	158 44	Gower et al. (1997)
		Picea mariana	49 24	390.36	61.60	445 76	Gower et al. (1997)
		Pinus banksiana	34 55	14.20	202.30	68.98	Gower et al (1997)
	Manitoba, Canada	*Populus* spp.	56 95	97.170	222.70	176.39	Gower et al (1997)
		Picea mariana	57.21	418.36	38 10	479.38	Gower et al. (1997)
		Pinus banksiana	28.99	25 78	136 00	68.37	Gower et al. (1997)

the boreal forest ecosystem carbon was stored in the soil (Gower et al 1997) This difference was more evident in the black spruce (*Picea mariana*) stands in Saskatchewan and Manitoba, Canada, and less evident in the aspen (*Populus* spp) or jack pine (*Pinus banksiana*) stands within the same region (Table 6.1) Aboveground carbon pools at five AmeriFlux sites in the forests of the eastern United States (Curtis et al 2002) differed significantly from those at more productive southern sites and from those in less productive northern hardwood sites in Michigan and Wisconsin (Table 6.1.). However, the Willow Creek Site in Wisconsin, which was dominated by aspen and northern hardwoods, had more soil carbon than other sites in the region (Curtis et al. 2002). In the southern hemisphere, old-growth Chilean forests were found to have greater biomass of coarse woody debris than most temperate forests other than those in the Pacific Northwest of North America (Schlegel and Donoso 2008).

6.3 Carbon dynamics in forested landscapes

Changes in carbon fluxes and storage across forested landscapes (i.e., across multiple ecosystems arranged in a cohesive mosaic) have been difficult to understand and measure due to the complex interactions between landscape structure and ecosystem processes and changes in these interactions over time. The two critical issues that must be accounted for in any landscape-scale research are heterogeneity and scaling Although both topics have received extensive attention during the past 20 years, much less effort has been spent on their relationship to carbon cycles, due mostly to the high costs of such studies and a lack of effective methods. At the ecosystem level, several mature methods (e.g., the eddy-covariance technique, biometric sampling, chamber-based flux measurement, ecosystem modeling) can provide us with reliable estimates of both fluxes and storage (Chen et al. 2004). However, scaling-up of ecosystem-level carbon fluxes and storage to a landscape level is not always accurate because of the presence of many smaller elements (e.g., corridors) and of interactions among patches (Desai et al. 2008).

Intensive measurements of carbon fluxes and storage for the dominant landscape elements have attempted to support scaling-up of the estimates to the landscape level (Chen et al 2004, Jenkins et al 2001, 2003, Pan et al. 2009, Smithwick et al 2009; Turner et al. 2011; Turner et al. 2004) For example, Euskirchen et al. (2003) measured the R_s, microclimate, and litter depth of six dominant patch types in a managed forest landscape in northern Wisconsin in 1999 and 2000 They found not only a significant difference among the patches but also a 37 % higher R_s in 1999 than in 2000, suggesting that the changes in any flux term over time must also be accounted for in any effort to understand the landscape-scale carbon cycle. A similar bottom-up approach for scaling up NEP was attempted by installing permanent and mobile eddy-covariance towers (Ryu et al 2008) in an effort to include heterogeneous patch types and their associated characteristics in landscape-scale estimates. This effort was assisted by a cross-lab collaboration that combined spatiotemporal

data from eddy-covariance towers (Desai et al 2008, Noormets et al 2008), R_s measurements (Martin et al. 2009), and models (Ryu et al 2008, Zhang et al 2012). However, the resulting carbon flux estimates remain problematic because no consideration was given to the influence of patch interactions or the contributions from minor elements of the landscapes (e.g., roads, small lakes). The results of these studies will nonetheless support scaling-up if they can be coupled with the spatially continuous characteristics of the landscape structure (Zheng et al. 2004) and will support the validation of modeled landscape-scale carbon fluxes and storage (Xiao et al. 2009).

Few studies have attempted landscape-level investigations of the carbon cycle. Several studies have been conducted in the Brazilian tropical forest region under the Large-Scale Biosphere-Atmosphere Experiment (http //lba.cptec.inpe.br/lba/site/). The researchers found that Amazonia constitutes a large global carbon store. Forest conversion in Amazonia is turning these forests into a net source of atmospheric carbon (Davidson et al 2012, Tian et al 1998) Recent measurements indicate that undisturbed Amazonian forest systems may be a net carbon sink, although the importance of carbon sequestration in regrowing forests on abandoned land is unclear (also see Pan et al. 2011) Dantas de Paula et al. (2011) found that carbon stocks varied greatly among landscape patches and that forest interiors retained nearly three times the carbon (202.8 ± 23.7 Mg C ha^{-1}) of forest edges due to edge effects They found that 92 % of the forest stored only half of its potential carbon due to fragmentation and the resulting edge effects, including wind damage and exposure to drought. These findings contradict those of a study in the Delaware River landscape, where fragmented landscapes had higher NPP (Jenkins et al. 2001). In Northern Wisconsin, a 395-foot-tall tower was used to directly measure the net exchanges of carbon, water, and energy in a landscape dominated by northern hardwoods (Bakwin et al. 1998, Chen et al. 2008). The NEP and R_e reported from this tower represent the cumulative values for an eddy-covariance tower with a fetch length greater than 10 km in which different ages and types of patches coexist. To scale up the results to a regional level, both aircraft-based flux measurements (Stephens et al. 2007) and intensive field campaigns were conducted to quantify the C fluxes and storage, including the Midwest Intensive Field Campaigns conducted by the North American Carbon Program (http.//www.nacarbon.org/nacp/)

Coupling remote sensing with ecosystem modeling and ground measurements of carbon fluxes and storage can also provide good estimates of carbon fluxes (e.g., Sun et al. 2011; Xiao et al. 2010, 2011) and pools (e g , Blackard et al 2008) at landscape, regional, and global scales because the emphasis is on the overall region, and several reliable satellites can cover the globe with a coarse resolution (e.g., MODIS). At the landscape scale (i e., tens of kilometers solution), no satellite data can quantify the parameters (e g , leaf area, microclimate) required to model carbon fluxes or storage with sufficient spatial or temporal resolution. Landsat imagery has the necessary spatial resolution (30 m), but has insufficient temporal resolution (due to the 16-day repeat cycle of the satellites and data gaps that result from cloud contamination) and measures only a limited number of spectral bands, thereby preventing accurate estimation of carbon gains and losses A few promising, high-resolution remote-sensing technologies are being tested in carbon cycle research, such as LIDAR (Chopping et al 2012, Parker et al. 2004) and AVIRIS (Roberts et al 2004), although application of the latter technology outside of the western countries remains difficult. Predictions of belowground carbon storage and carbon fluxes based on remote sensing are not feasible Consequently, our current knowledge of landscape-scale carbon fluxes and storage is based on the predictions of ecosystem models (e.g., belowground carbon; Gower et al. 1997) or on spatial interpolations between point estimates (e.g , Euskirchen et al 2002; Pan et al 2009, Turner et al. 2004, 2009)

A small handful of studies were conducted to link landscape structure with key carbon fluxes or storage pools (Jenkins et al. 2001, Noormets et al. 2007, Turner et al 2004, Zheng et al. 2004) Based at the Chequamegon National Forest in Wisconsin, Zheng et al (2004) produced a high-resolution map of stand age calculated from field measurements of tree diameter. Various vegetation indices were derived from Landsat 7 ETM+ imagery through multiple-regression analyses to produce an initial AGB map. This study is among the few in which AGB was estimated over a long study period (here, 30 years) based on near-infrared reflectance and the normalized-difference vegetation index. However, carbon fluxes and storage from other ecosystem components (e.g., the soil) may not be determined using this approach.

Scaling-up from trees and stands to landscapes (i.e., a bottom-up approach) appears to be more plausible than satellite-based approaches because many smaller structural elements cannot be quantified even from Landsat images, such as smaller woodlands, areas of edge influence (AEI, i.e., areas along the edges of fragmented stands where edge effects are significant), riparian zones, and narrow corridors. These structural features may be the dominant features of a landscape (e.g., dotted woodlands in the Midwest region of the United States) or may play significant roles in estimating landscape-scale carbon fluxes and storage. For example, integrating the terrestrial and aquatic components of regional carbon budgets in managed landscapes has been among the research foci (cf Buffam et al. 2011). Giese et al. (2003) investigated the carbon pools of a managed riparian forest in the coastal plains of South Carolina and found a high potential for carbon storage, especially as BGB. A recent study by Rheinhardt et al. (2012) found that the carbon stored in riparian zones in the headwater reaches of a watershed in an agriculture-dominated landscape amounted to only about 40 % of the potential capacity.

As another example, forests influenced by clearcut edges were found to be responsible for a 36 % reduction of biomass in a Brazilian tropical forest (Laurance et al. 1998). Zheng et al (2005) used the changes in land cover type and composition from 1972 to 2001 and an R_s model to assess the contribution of AEI to carbon emission in the Chequamegon National Forest in Wisconsin They found that changes in land cover increased landscape R_s by approximately 7 % during the 30-year period. This is likely to be significant because of the large portion of AEI in the landscape. However, these pioneering studies are far from providing a compre-

hensive understanding of all major carbon fluxes and storage After 14 years of investigating the Chequamegon National Forest landscape (Chen et al 2006), we are still incapable of predicting the carbon fluxes and storage in AEI, roadside areas, riparian forests, and lakeshore forests Li et al. (2007b) found that the total AEI amounted to approximately 48, 74, 86, and 92 % of the landscape with the depth of edge influence (i.e., the distance inside a forest stand to which the edge effect is significant) set at 30, 60, 90, and 120 m, respectively AEI and roads accounted for 48 and 8 %, respectively, of the landscape in this study area, and their proportions had increased from 1972 through 2000 (Bresee et al 2004). Across the United States, the total amount of AEI accounts for 42 8 % of our national forests (Riitters et al. 2002), but its contribution to the landscape carbon cycle remains unknown (Harper et al. 2005)

There are also many ignored landscapes for which our knowledge of carbon fluxes and storage is limited. This list includes urban areas, despite the important effects of intensive management, direct interactions between human populations and their environment, and the high potential of these areas to sequester carbon. This gap in our knowledge is particularly important because urban areas are growing at a faster rate than any other land-use type (Lal and Augustin 2012). Peters et al. (2011) argued that urban areas contributed 71 % of global energy-related CO_2 emissions in 2006. The United Nations reported that the global urbanization rate (i e., the proportion of the population living in cities) was 49.6 % in 2007 and is expected to reach 70 % by 2050 (http·//esa.un.org/unpd/wup/index.htm). Almost all of this increase will come from urbanization of developing countries, providing both a challenge and an opportunity to manage carbon emissions. Davies et al. (2011) examined the quantities and spatial patterns of AGB in Leicester, UK, after surveying vegetation across the entire urban area and reported storage of 3.16 kg C m^{-2}, with 97.3 % of this pool being associated with trees rather than with herbaceous and other woody vegetation. McKinley et al. (2011) stated that the carbon density of urban landscapes in the United States was similar to that of tropical forests. In summary, it is clear that the structure of and changes in land mosaics are important components of landscape-level carbon fluxes and storage (Noormets et al 2007, Turner et al. 2009). Yet despite this importance, there remain many knowledge gaps for predicting the carbon cycle at this scale.

6.4 The roles of climate and disturbance

Forests and landscapes are not static, rather, they are constantly changing, resulting in large temporal changes in carbon fluxes and storage. Three driving forces for these changes often act together (Caspersen et al. 2000, Pan et al. 2009, Smithwick et al. 2009): changes in the environment (e.g., climate, soil, atmospheric chemistry) of the ecosystem or landscape, natural disturbances, and management practices.

6.4.1 *Climate change and the carbon cycle*

Global climate change now appears to be inevitable and will have profound impacts on natural ecosystems at all spatial scales The feedbacks between forests and climate are complex, but a unique characteristic among the multiple feedbacks results from the longevity of trees and forests. Trees, in general, seem to be more tolerant of change than shrubs and herbaceous species (i e., they exhibit relatively slow responses), but fast responses of carbon fluxes and storage to climate change have been widely reported because climatic factors directly regulate all flux terms for a forest ecosystem (Chen et al. 2002). The "fertilization" of trees by increasing atmospheric CO_2 will mostly likely enhance GPP (Pan et al 2009), but elevated temperatures caused by increasing atmospheric concentrations of CO_2 and other greenhouse gases (CH_4 and N_2O) will also promote respiratory losses (R_e), resulting in an uncertain change in NEP (Bonan 2008).

Large-scale experiments to simulate the effects of climate change (CO_2, O_3, temperature, precipitation) have been initiated in several forests, including the cool-temperate Harvard Forest (Melillo et al 2011), a poplar plantation in northern Wisconsin (Karnosky et al 2003), and a loblolly pine plantation in the Duke Forest (Ellsworth et al. 2012, Oren et al. 2001), but the results from these experiments pointed to different trends for the different flux terms, with great uncertainties. One primary reason for the uncertainty is that no experiment has considered more than three factors related to the future climate due to the complexity and high costs of such modeling. Consequently, these predictions will need to be based on validated models. Interestingly, climatic extremes are predicted to be one of the major consequences of climate change, yet little is known about the effects of climate extremes on ecosystem processes (Ciais et al 2005, Xiao et al. 2009), especially if multiple extreme events occur simultaneously (e.g , a heat wave plus drought). Although much experimental work has been conducted on the effects of chronic warming on ecosystems, most of these experiments were (understandably) conducted with short vegetation such as grasses and shrubs (e.g., Hovenden et al 2008, Shaw et al. 2002) Few past studies have examined the effects of acute heat stress (short-term, high-temperature events) on naturally occurring vegetation (Melillo et al. 2011) Recent reviews have highlighted the significant negative impacts of heat stress on trees and forests (Allen et al. 2010, Rennenberg et al. 2006) In addition, researchers have not examined how landscape heterogeneity will respond to the changing climate, adding one more challenge for predicting changes in carbon fluxes and storage

The responses of carbon fluxes and storage in forest ecosystems and forested landscapes to climate change are difficult to predict because the underlying mechanisms are much more complex than previously thought. Several particularly vexing challenges associated with climate change raise the following questions·

1. How the impact of climate change will extend beyond the effects of chronic warming and CO_2 fertilization to include interactions among multiple factors

(e g , O_3, N deposition) and extreme physical and biological events (e g., drought, asymmetric warming, Gutschick and Bassirirad 2010, IPCC 2007)?
2. How significant variation in both the driving forces and the ecosystem responses across temporal and spatial scales will affect forest processes (Jung et al. 2010, Martinez-Meier et al. 2008, Xiao et al 2010)?
3. How our knowledge of the regulatory mechanisms for different fluxes that arise from feedbacks among the driving processes must be improved to allow these mechanisms to be incorporated in ecosystem models?

Ecosystem models have become increasingly important tools to answer these questions. Hundreds of ecosystem models have been developed during the past four decades and all have included a range of components in the carbon fluxes and storage pools. However, comparisons among the models and validation against field measurements of carbon fluxes and storage indicate that none of the models can be reliably applied to all ecosystem types or at all scales (Schaefer et al 2012) Landscapes are composed of multiple ecosystem types, thus the modeling community faces the challenge of developing a new generation of models that accounts for this diversity. Another frontier in addressing landscape-scale responses to the changing climate will be to develop location-specific predictions of the future climate so that ecosystem models can be properly parameterized (e g., regional downscaling modeling; Spak et al. 2007). This is because the spatial resolutions of the current global circulation models are too coarse (>100 km) and therefore cannot capture the effects of heterogeneous landscape elements, which frequently act at resolutions as low as 10 m. One well-known exercise is the Wisconsin Initiative on Climate Change Impacts (http://www.wicci.wisc.edu/), in which high-resolution regional predictions are being made to assess the impacts of climate change on Wisconsin's ecosystems. The program combines cutting-edge climate modeling capabilities with field expertise to assess the impacts on forest production, biodiversity, and the development of practical decision-support information at fine scales.

6.4.2 *Disturbance and the carbon cycle*

The responses of the carbon cycle of forested landscapes to natural disturbances have received much attention (Amiro et al. 2010, Balshi et al 2009, Goetz et al. 2012, Kurz et al. 2008, Turner 2010). This is because natural disturbance often changes the landscape structure immediately, resulting in rapid changes in the magnitudes and directions of carbon fluxes and storage. Wildfires, outbreaks of insects and diseases, and windstorms are among the major natural disturbances in the northern hemisphere that have profound effects on forest carbon cycling (Amiro et al. 2010). Worldwide, fire is a key influence on global vegetation patterns, and especially on the distribution of forests; in the absence of fire, forest cover would about double, from 27 % of the vegetated land surface to 56 % (Bond et al. 2005). Thus, fire also has a profound influence on carbon storage.

Wildfires have been the most important disturbances in many regions. They not only directly produce carbon loss during the burn but also produce significantly different environments that, in turn, change the magnitudes and directions of subsequent carbon fluxes Gower et al. (1997) used an ecosystem model to simulate the carbon balance of the Canadian boreal forest since the 1930s and found that the effects of CO_2, temperature, and precipitation varied interannually but generally balanced out over long time periods and large areas Forest fires during this period had the greatest direct impact on carbon emissions from the system Balshi et al. (2009) estimated that decadal-scale CO_2 emission caused by fires in the boreal region of North America will increase to 2 5 to 4.4 times the present level by the end of this century. Vasileva et al (2011) found that wildfires in central Siberia are among the major factors driving the short-term (synoptic) variability of near-surface CO_2 during the warm season. At the stand level, Concilio et al. (2006) found that R_s not only varied in response to fire intensity but that its spatial and temporal variations were also greatly dependent on the patch patterns of the understory vegetation One of the best examples of alteration of the carbon cycle at the landscape level is from Yellowstone National Park, where large wildfires in 1988 burned 47 % of the lodgepole pine (*Pinus contorta*) forests, a major forest type in the park that is prone to fires; it covers a total area of 525 000 ha. These fires caused a loss of 13 6 Mg C ha^{-1} (Kashian et al 2006, Turner et al. 2004) However, postfire carbon accumulation can be rapid relative to historical fire intervals In the park, about 80 % of the prefire carbon is typically recovered within 50 years and 90 % is recovered within 100 years, although ecosystem carbon is sensitive to variations in stand structure (e g , basal area) and stand age (Kashian et al 2013). Forests in the park would store substantially less carbon, however, if fire intervals decreased substantially as the climate warms (Westerling et al. 2011).

Deforestation caused by timber harvests, fuel-reduction treatments, and other types of land management are major anthropogenic disturbance agents that shape carbon cycles in the world's forested landscapes Compared to natural disturbances, the influences from human activities on carbon cycling are direct, dramatic, extensive, and sometimes long lasting. For example, rainforest fragments in central Amazonia have been found to experience a marked loss of AGB caused by sharply increased rates of tree mortality and damage near the margins of the residual patches (Laurance et al. 1998). In the eastern United States, the current high carbon storage and NEP in forests are the consequences of forest regrowth after large-scale clearing of these forests between 1860 and the 1960s (Pan et al. 2009). However, management protocols during the late twentieth century were designed to maximize timber production, control erosion, prevent wildfires, and conserve species diversity With increased awareness of other ecosystem services, such as carbon sequestration, our current challenge is to revisit the conventional management protocols at both stand and landscape levels to sustainably achieve multiple objectives.

Our knowledge of the carbon cycles in forested landscapes is not solely about the magnitudes of carbon fluxes and storage but also about how they change over time Obviously, both human and natural disturbances must be included in the conceptual framework. These changes were first discussed in the pioneering research of

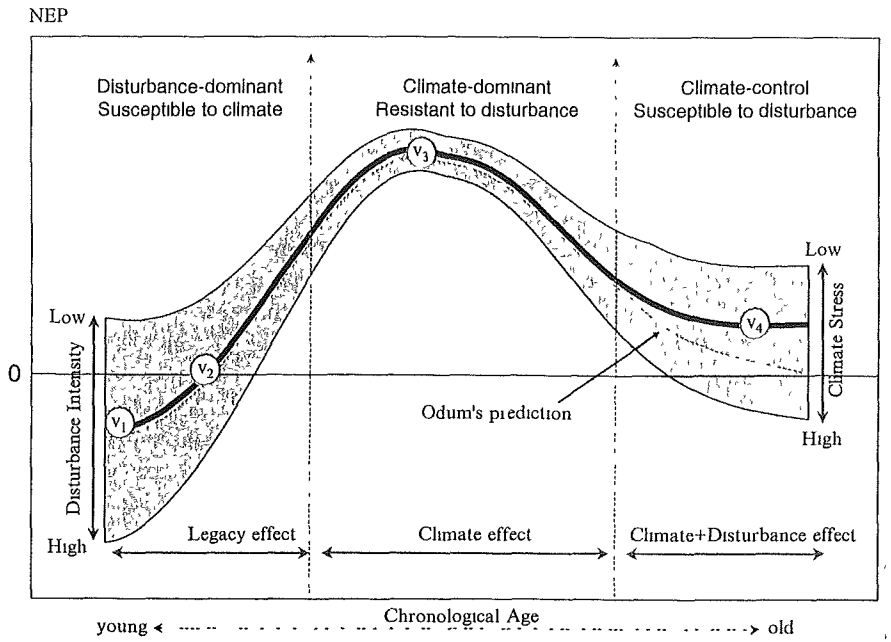

Figure 6.2 A hypothetical framework for predicting the changes in net ecosystem productivity (NEP) caused by climate variation superimposed on the effects of disturbances as a function of the time following a disturbance and four different stages (V_1 to V_4)

Odum (1969), but research has expanded greatly during the past two decades (Amiro et al. 2010, Chen et al. 2004, Euskirchen et al. 2006, Gough et al. 2008a, Harmon et al. 1990, Kashian et al. 2006, Pregitzer and Euskirchen 2004, Turner et al. 2011). Here, we offer a brief hypothetical discussion of NEP given that much of the current attention is on the strength of forest sequestration of carbon (i.e., on the magnitude of NEP).

Although the general predictions of Odum's (1969) succession theory explain ontogenetic changes, they do not address the variability among stands. Direct measurements of NEP have shown that considerable variability exists between stands of similar ages and developmental stages. A disturbance event is thought to move a stand forward or backward within the successional time series. The implicit assumption is that the sequence of conditions that constitute the successional series is constant and invariant. Here, we propose an alternative view, a three-stage conceptual framework based on the changes in NEP after a disturbance (Fig 6.2).

During Stage 1 (V_1, Fig. 6.2), the nature and severity of a preceding disturbance are likely to be the major determinants of the ecosystem carbon balance. The increase in respiration caused by an increase in dead organic matter, changes in soil compaction and aeration, and changes in the ecosystem energy balance relative to

the decrease in assimilation caused by a reduction in the effective leaf area and an altered radiation balance that affects the ratio of evaporation to transpiration may vary greatly depending on the disturbance type, disturbance intensity, and prior site conditions. Consequently, the range of variation of NEP is high during this stage (see Amiro et al. 2010, Chen et al. 2004, Euskirchen et al. 2006, Gough et al. 2008a). As legacy effects weaken during subsequent stand development and as respiration becomes dependent on new carbon inputs, the stand enters Stage 2 (V_2, Fig. 6.2), in which the magnitude of NEP depends most strongly on ecosystem composition and structure and NEP is increasingly sensitive to variations in climate. During late-successional stages (V_3 and V_4, Fig. 6.2), as the trees reach and pass their age of maximum growth rate, the site's nutrient and water availability are likely to render the forest increasingly susceptible to climate anomalies. Recently, scientists concluded that old-growth forests absorb substantial amounts of CO_2 from the atmosphere (Carey et al. 2001, Luyssaert et al. 2008)—a finding that contradicts Odum's theory and that has been touted as the basis for a global forest carbon management policy based on the preservation of these communities. However, with increasing mortality of overmature trees, the utilization of the dead organic matter in respiration will respond more strongly than assimilation to climate fluctuations, contributing to greater interannual variability of NEP (Chen et al. 2002, Gough et al. 2008a). Clearly, late-successional ecosystems have higher interannual variability in NEP that depends strongly on variations in the relationship between climate and disturbance.

Our hypothetical framework can be summarized as follows: variation in ecosystem NEP during the early development stages is primarily determined by the nature and severity of the preceding disturbance event (i.e., a legacy effect), the effects of climatic variability on NEP are most significant during the late-successional stages, and stands in intermediate developmental stages are most resilient against these influences and their NEP is determined most tightly by intrinsic vegetation properties and edaphic constraints.

The carbon cycle has long been a core component in many large-scale manipulative experiments that evaluated alternative management options. For example, the carbon sequestration capacity of a forest is broadly determined by the balance between its photosynthetic gains and its respiratory losses. To maintain optimal short- and long-term sequestration rates, the forest can be managed by retaining sufficient trees (i.e., leaves) to maintain a high rate of photosynthesis and provide a good buffer for the understory and soil microclimate (e.g., decreased respiration through lowered temperature). The foundation for this framework is that forests can be managed best by maintaining high photosynthetic rates (i.e., carbon gain) by retaining a sufficient number of green trees (i.e., leaves) and by reducing ecosystem respiration (i.e., losses) by moderating the forest and soil microclimate and structure. In the Missouri Ozark Forest Ecosystem Project, we first examined the changes in carbon storage under different management regimes and found that single-tree uneven-aged management and clearcut even-aged management of stands reduced

total carbon storage from 182 Mg C ha^{-1} to 170 and 130 Mg C ha^{-1}, respectively. Although these changes are expected due to the removal of timber from the sites, the harvests reduced carbon pools in live tree biomass by 31 % under uneven-aged management and by 93 % under even-aged management, and increased coarse woody debris carbon pools by 50 % under uneven-aged management and by 176 % under even-aged management compared with the levels in the absence of harvesting (Li et al. 2007b). In a parallel study, Concilio et al. (2005) found that selective thinning in an experimental forest in the Sierra Nevada Mountains produced a similar effect on both mixed coniferous and hardwood forests by elevating soil respiration, moisture content, and temperature and, consequently, thinning increased R_s by 14 %. Xu et al (2011) found that the summer mean R_s and soil moisture tended to be higher in wet years (2004, 2006, and 2008) and lower in dry years (2005 and 2007) under even-aged and uneven-aged management than in unharvested stands in the Missouri Ozark Forest Ecosystem Project experiment. Li et al. (2012) reported a significant difference in the various respiration fluxes among the treatments in this study. Altogether, it is clear that these management activities changed not only the total storage and carbon distribution in the forest but also the magnitudes and temporal dynamics of the carbon fluxes

Landscape management, by definition, will alter the landscape's spatial heterogeneity and will consequently change both carbon pools and fluxes However, we found only a few manipulative landscape studies that linked structural changes and carbon pools, preventing us from developing sound landscape-level management guidelines that would let managers design the temporal and spatial characteristics of landscape mosaics (Chen et al. 2006) Several investigations concluded that forest fragmentation and the resulting edge effects will produce negative impacts on carbon sequestration (e g., Dantas de Paula et al 2011). Therefore, future management should be designed to reduce fragmentation, a recommendation that agrees with the guidelines for conservation of biological diversity (Harper et al. 2005). Nevertheless, our knowledge of how alternative landscape patterns will affect the carbon cycle is still lacking.

6.5 Outlooks

Carbon studies have gained tremendous momentum in the past two decades because of their central roles in many pressing global issues that face society, such as climate change, energy security, shortages of natural resources, and rapid growth of the world's population and the global economy. Forest ecosystems will increasingly play a critical role in these issues, in large part due to the large carbon fluxes and storage in terrestrial ecosystems. Based on our literature review, future research on the carbon cycle in forested landscapes should be strengthened in the following three areas

6.5.1 *Temporal and spatial dynamics of carbon*

The carbon cycle in forest ecosystems has been investigated for decades, yet there remain many unknowns about the distribution, temporal changes, and regulatory mechanisms for carbon other than the effects of climate. For example, the distributions and dynamics of carbon in complex terrain are characterized by many small carbon fluxes that are incompletely understood (Fig 6 1). Limited data and knowledge are available regarding carbon dynamics in some ecosystem components (e g., deep soils, wetlands, the urban–rural interface, the land–ocean interface, and other critical zones) From a theoretical perspective, the predictions by Odum (1969) about the responses of the carbon cycle after a disturbance have been challenged because of a lack of thorough validation Although significant progress has been made in genetics, population and community ecology, and carbon cycle science, consensus on the interactions between the diversity of a forest ecosystem and ecosystem function has not been reached. Finally, understanding the carbon cycle more holistically by including indirect drivers and feedbacks should be explored

6.5.2 *Landscape-scale carbon cycles*

Our understanding of carbon fluxes and storage at the landscape level has lagged significantly behind our knowledge at ecosystem and landscape levels. This is partially due to the limitations of existing methods and technology, which are both costly and labor intensive Sound landscape-scale experiments have not been widely pursued, thus testing and validation of the basic concepts and principles of landscape ecology have been inadequate. Although carbon and water fluxes and storage are well coupled in both vertical and horizontal dimensions (Govind et al. 2010, Ju and Chen 2005, Sun et al. 2011), sound estimates of the horizontal flows of carbon as well as their relationship to landscape-scale processes are rare in current models This lack of a satisfactory landscape-scale perspective is particularly unfortunate because most forests are owned and managed at a landscape level, and fragmentation is on the rise. Innovative proposals that can overcome these scientific and management challenges are urgently needed

6.5.3 *Humans and carbon cycles*

The relationships between carbon sequestration and societal issues (e g., global warming, fire management, urban growth) need to be studied more intensively from a more holistic perspective that couples humans with the natural systems that sustain us. The traditional approach of linking forest management and carbon cycles independently of human influences must be expanded to include functions that

are relevant to human society, such as society's needs for carbon management (e.g., stock markets, biological conservation, bioenergy) and conservation of other ecosystem services.

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Chapter 7
Forest landscape change and biodiversity conservation

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Abstract Forest landscapes are changing at unprecedented rates in many regions of the world. This may have profound consequences for the diversity and resilience of forest ecosystems and may impose considerable challenges for their management. In this chapter, we review the different types of change that can occur in a forest landscape, including modifications in forest habitat amount, quality, fragmentation, connectivity, and heterogeneity. We describe the conceptual differences and potential interactions among these changes and provide a summary of the possible responses of forest species depending on their degree of habitat specialization, dispersal abilities, and other factors. We review the main current drivers of change in different regions of the world and how they are affecting (often synergistically) forest biodiversity: deforestation, climate change, forest fires, abandonment of rural land, land-use intensification, spread of invasive species, forest management, and the increasing amount of plantation forest We conclude by providing a summary of recommendations and strategies for mitigating and minimizing the undesirable effects of landscape change on forest biodiversity.

7.1 Introduction

Despite increasing conservation efforts (Rands et al. 2010), global biodiversity, which comprises the diversity of life in all its forms and levels of organization (Hunter and Schmiegelow 2011), has declined in recent decades (Butchart et al 2010)

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