Chapter 3
Forest Processes

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3.1 Introduction

Some of the changes to U.S. forests will be directly caused by the effects of an altered climate, such as increases in atmospheric carbon dioxide (CO_2) temperature (T), and nitrogen (N) deposition on tree growth, mortality, and regeneration.

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Other changes will be indirectly caused by climate-induced changes in disturbances, such as droughts, fire, insect outbreaks, pathogens, and storms (see Chap. 4). In this chapter, we document current knowledge of the potential direct of climate change on biogeochemical cycling (i.e., carbon [C], nutrients, and water) and forest tree distributions.

3.2 Carbon and Nutrient Cycling

The United States has about 303 million ha of forest land, about 8 % of the world's total (see Chap. 5). Forest C stocks and uptake or loss rates differ greatly across a wide range in environmental conditions, land use, land-use history, and current human influences (see Chap. 7). Forests of the conterminous United States cover about 281 million ha and contain 45,988 Tg C. Estimates of the amount of CO_2 emissions (1,500 Tg C in 2009) offset by forests and forest products in the United States vary from 10 to 20 % depending on assumptions and accounting methods (McKinley et al. 2011), with 13 % being the commonly used estimate as of 2011 (USEPA 2011). Ninety-four percent of forest C storage comes from growth on current forest lands, with the remaining 6 % from a net positive conversion of other land uses to forests. Regional differences in forest C pools and storage rates are reported in McKinley et al. (2011); Woodbury et al. (2007), and U.S. Environmental Protection Agency (USEPA) (2011). Updates of the inventories used to estimate these pools and storage rates may be important to capture C losses in recent large fires, bark beetle outbreaks, and drought mortality. Components such as dead wood and C in soil are either sparsely measured or are only estimated (Woodbury et al. 2007).

These forest C storage estimates are similar to those reported in a global study of forest sinks derived from the same sources (Pan et al. 2011). An analysis using eddy covariance flux measurements, satellite observations, and modeling estimated annual C storage in the conterminous United States as 630 Tg C year^{-1} (Xiao et al. 2011), largely from forests and savannas; most agricultural lands either store little additional C or lose C (USEPA 2011). The large discrepancy between the biometric USEPA estimates and those of Xiao et al. (2011) is probably caused by: (1) woodland encroachment (Van Auken 2000; Pacala et al. 2001; McKinley and Blair 2008) not measured by the U.S. Forest Service Forest Inventory and Analysis used for the USEPA reporting, and (2) poor performance of eddy

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covariance measurements in estimating ecosystem respiration (Barford et al. 2001; Bolstad et al. 2004; Kutsch et al. 2008; Wang et al. 2010). Other estimates for the conterminous United States are 1,200 ± 400 Tg C year^{-1} from inversion analysis (Butler et al. 2010) and 500 ± 400 Tg C year^{-1} from three-dimensional atmospheric CO_2 sampling (Crevoisier et al. 2010).

3.2.1 Response of Forest C Cycling to Changing Environmental Conditions

Carbon storage in forest ecosystems results from the balance between growth of wood, foliage, and roots and their death or shedding and subsequent decomposition. Temperature, atmospheric CO_2 concentration, ecosystem water balance, and N cycling all interact to alter photosynthesis and growth. For example, higher temperatures can benefit growth, but the most benefit would come with adequate nutrition and soil water. Disturbance rapidly changes the balance between production and decomposition, but chronic changes in temperature, precipitation, CO_2, and N deposition over large areas can also alter C balance over longer time periods.

Experiments and measurements provide insights into forest C balance. Atmospheric concentrations of CO_2, currently near 400 ppm, are expected to rise to 700–900 ppm by 2100, depending on future emission scenarios and any changes in atmospheric uptake by terrestrial and aquatic ecosystems. Experimental results confirm that the primary direct effect of elevated CO_2 on forest vegetation is increased photosynthesis (Norby et al. 2005), but individual studies show that photosynthetic enhancement, growth and C storage are moderated by water and nutrient availability (Finzi et al. 2006; Johnson 2006; Norby et al. 2010; Garten et al. 2011). Free-air CO_2 enrichment studies (Norby and Zak 2011) show that (1) elevated CO_2 does not increase leaf area in forests, (2) net primary production (NPP) is enhanced under elevated CO_2 only when water and nutrient supplies are abundant, (3) water use is reduced through stomatal closure (Leuzinger and Körner 2007; Warren et al. 2011), and (4) CO_2-promoted increases in photosynthesis and NPP do not always increase forest C storage.

Elevated atmospheric CO_2 will likely increase forest productivity, although the magnitude of increase will be affected by how elevated CO_2 will affect belowground processes (Lukac et al. 2009), mature trees, and wetlands. For example, recent study suggests that, a 19 % increase in CO_2 over the past 50 years may have increased quaking aspen (*Populus tremuloides* Michx.) growth more than 50 % (Cole et al. 2010). Elevated CO_2 commonly enhances soil CO_2 efflux, suggesting that some of the additional photosynthesis is rapidly cycled back to the atmosphere (Bernhardt et al. 2006). An increase in labile C in soil may increase decomposition and potentially reduce soil C storage (Hofmockel et al. 2011). In a mature forest, sustained increases in photosynthesis in response to elevated CO_2 (Bader et al. 2009) did not increase wood growth (Körner et al. 2005), soil respiration (Bader and Körner 2010), or root

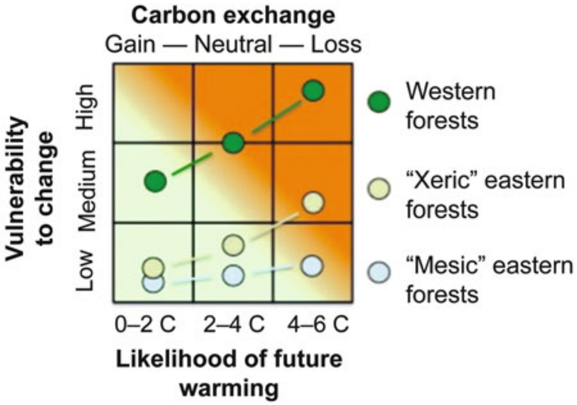


Fig. 3.1 Risk analysis diagram for the forest C cycle. Western forests are considered inherently limited by water demands that exceed precipitation supplies during substantial portions of the year. Xeric Eastern forests include those growing on shallow or coarse-textured soils or those present at the prairie-forest transition zone that experience water deficits in some years. Mesic Eastern forests experience severe water deficits only in occasional years and for relatively brief periods

or soil C storage (Asshoff et al. 2006; Bader et al. 2009). In wetlands, elevated CO_2 can increase CO_2 and methane efflux (Ellis et al. 2009), but these fluxes interact with hydrologic cycling and potential species changes (Fenner et al. 2007).

In temperate and boreal forests, modest increases in temperature tend to increase growth (Way et al. 2010) (Fig. 3.1). Warming will probably enhance upland forest growth for ecosystems with ample water, through changes in plant development and a longer growth season (Hänninen et al. 2007; Bronson et al. 2009; Gunderson et al. 2012). Growth in water-limited ecosystems will probably be reduced (Hu et al. 2010; Arend et al. 2011), and net C storage may be reduced (Cai et al. 2010). Warming will also enhance microbial decomposition and nutrient mineralization in soils (Melillo et al. 2002), increasing plant nutrient availability (Melillo et al. 2011), but the long-term tradeoff between soil C loss and nutrient-enhanced productivity is unknown. A longer growing season may increase the possibility of damage to trees from late frost events (Gu et al. 2008; Augspurger 2009).

Eastern forests, particularly on deep soils, are well buffered against substantial reductions in precipitation; forest growth, soil C storage, and nutrient availability show little effect of a chronic 12-year, 33 % reduction in precipitation (Hanson et al. 2007; Froberg et al. 2008; Johnson et al. 2008). Forests that rely on snowmelt for water will probably grow less in drier conditions (Boisvenue and Running 2010; Hu et al. 2010), and more frequent droughts in Western forests will reduce tree growth, vigor, and survival (McDowell et al. 2008; McDowell 2011). Precipitation amount may be more important for forest productivity than its frequency and intensity (Gerten et al. 2008).

In areas where N deposition increases, it may enhance ecosystem C storage by increasing forest productivity (Churkina et al. 2009; de Vries 2009) and decreasing decomposition of soil organic matter (Janssens et al. 2010), but those gains may be offset by the concurrent release of nitrous oxide, a potent greenhouse gas (Zaehle et al. 2011). The potential for enhancing C gain would be low in regions where N deposition is already high (e.g., the Northeast) and high in regions where N deposition is low (e.g., the Southwest). Tree species have a wide range of susceptibility to tropospheric ozone, which also varies regionally, and damage caused by ozone is not completely offset by elevated CO_2 (Karnosky et al. 2005).

Modeling has also been used to provide insights into forest C balance. Forests in different regions will probably respond differently to climate change because of variation in species composition, water and nutrient availability, soil depth and texture, and strength of other environmental factors such as ozone and N deposition. Understanding how these multiple factors will interact is difficult to test experimentally or measure, so modeling approaches are often used. In the eastern United States, model output suggests that productivity or forest C storage will increase with projected changes in climate, N, and CO_2, especially if precipitation increases, promoting higher photosynthesis under increased temperature. For example, upland oak forests in Tennessee are projected to increase their current C storage rate by 20 % for the climate and atmosphere projected for 2100 (CO_2 concentration 770 ppm, ozone concentration 20 ppb higher than today's level, 4 °C temperature increase, 20 % winter precipitation increase) (Hanson et al. 2005). Globally, temperate forest and grassland NPP is projected to increase 25–28 % for CO_2 concentration of 550 ppm (Pinsonneault et al. 2011), an estimate that includes expected changes in climate. Based on a four-model simulation of the effects of increased temperature and CO_2 and altered precipitation, Eastern forests showed increases in net C storage rates and net ecosystem production (Luo et al. 2008), and forest productivity increased specifically in the Northeast (Campbell et al. 2009).

For the western United States, models vary in their projections of productivity and C storage in forests. For example, changes in climate and CO_2 are projected to turn Rocky Mountain forests into a C source by 2090 (Biome-BGC model) (Boisvenue and Running 2010), and decrease forest C storage for boreal aspen (Grant et al. 2006), whereas other models project increased C storage for Western forests (CENTURY Model) (Smithwick et al. 2009; Melillo et al. 2011; Pinsonneault et al. 2011). Carbon in northern bogs, peat lands, and permafrost regions may be lost with a warming climate (increasing methane production), depending on hydrology and other factors (Heijmans et al. 2008; Ise et al. 2008; Koven et al. 2011). Global model simulations of climate change and ecosystem productivity (Friend 2010; Pinsonneault et al. 2011) project higher C storage for both eastern and western United States forests, with the larger increase in the East. It is important to note that none of these simulations consider the effects of altered disturbance regimes. For example, in the West, climate-driven increased fire and bark beetle outbreaks are likely to reduce forest C storage (Westerling et al. 2006, 2011; Metsaranta et al. 2010), jeopardizing the current U.S. forest sink (see Chap. 4). Recent large fires have already turned Arizona and Idaho forests from a C sink to a C source (USEPA 2011). Reduced tree vigor caused by drought and elevated temperature has promoted bark beetle outbreaks, resulting in short-term C loss for some forests in the West (Allen et al. 2010). Limited data suggest that mortality, perhaps related to climate, has increased slightly in some older forests in the West (van Mantgem et al. 2009). Little information on tree mortality trends exist for the eastern United States, but tree mortality in some forests in this region are sensitive to air pollution (Dietze and Moorcroft 2011). Tree regeneration after disturbance, which is critical for maintaining forest cover and associated C stocks (McKinley et al. 2011), is uncertain for Western montane forests in a warmer climate (Bonnet et al. 2005), especially if fire severity increases (Haire and McGarigal 2010).

3.2.2 Effects on Nutrient Cycling

Carbon cycling responses to elevated CO_2 and warming will be linked to nutrient availability, especially N. Biological processes that convert nutrients held in organic matter to available mineral forms are generally temperature dependent. Experimental soil-warming studies confirm that N mineralization will increase in response to higher temperatures (Melillo et al. 2011), with an average increase in net N mineralization of about 50 % (Rustad et al. 2001). These effects may be transient, however, because the supply of mineralizable substrates may not keep pace with opportunities for mineralization. Soil-warming studies are limited by methodological constraints that make it difficult to scale results to ecosystems or incorporate system interactions. However, modeling approaches that scale to the ecosystem and incorporate interactions have generally confirmed patterns observed in soil-warming experiments (Campbell et al. 2009). Recent studies have used observed climatic variability and corresponding measures of stream N in forested watersheds to infer changes in N cycling processes. For example, in the western United States, recent warming temperatures have melted glacial ice, subsequently flushing N from microbially active sediments (Baron et al. 2009). In the eastern United States, Brookshire et al. (2011) found that seasonal variation in stream nitrate was coupled with recent warming, and used modeling to project that higher temperature will increase future N export threefold more than will projected changes in N deposition.

Altered species composition can affect belowground nutrient cycling processes (Lovett et al. 2006; Knoepp et al. 2011). For example, forests with beech bark disease have increased litter decomposition, decreased soil C:N ratio, and increased extractable nitrate in the soil and soil solution (Lovett et al. 2010). In eastern hemlock (*Tsuga canadensis* [L.] Carrière) stands infested with hemlock woolly adelgid (*Adelges tsugae* Annand), litter N is increased, and N mineralization is accelerated even before tree mortality is observed (Stadler et al. 2006; Orwig et al. 2008). Defoliation by insects also alters N pools and fluxes in forests (Lovett et al. 2002).

3.3 Forest Hydrological Processes

Climate change will have both indirect and direct effects on forest water hydrologic processes. Indirect effects, which work primarily through effects on forest evapotranspiration (ET), are associated with changes in atmospheric CO_2, increased temperature, altered soil water availability, changes in species composition, and changes in disturbance regimes or management that alter forest structure and composition. Direct effects are associated with more rainfall and more intense storms in some regions (see Chap. 4). These in turn increase base flows in streams (particularly intermittent streams), increase flood risk, accelerate erosion, and increase the potential for both landslides and increased inter-storm periods and drought, along with climate-related changes in infiltration rate. Indirect and direct effects are interdependent.

3.3.1 Forest Evapotranspiration and Streamflow

Forest ET may be responding to changing climate (Labat et al. 2004; Walter et al. 2004; Gedney et al. 2006), but studies disagree about the direction of the change. Over relatively large areas and long temporal scales, streamflow is the balance between rainfall input and ET. Hence, the rainfall not used in ET is available for streamflow and groundwater recharge, and in many forest ecosystems, ET strongly influences streamflow and groundwater recharge. Walter et al. (2004) concluded that ET has been increasing across most of the United States at a rate of 10.4 mm per decade (inferred from U.S. Geological Survey records of precipitation and river discharge in six major basins). In contrast, river discharge throughout the East has been increasing at a rate of 4 % for each 1 °C increase in temperature (Labat et al. 2004), suggesting a reduction in ET. Different response patterns are not unexpected because ET is affected by several co-occurring and often counteracting climatic, physiological, and structural variables. For example, increased discharge (Labat et al. 2004) has been attributed to the physiological effect of CO_2 on water use efficiency (thereby decreasing ET), and not to the effect of changing land use (Gedney et al. 2006).

3.3.2 Elevated Atmospheric CO_2

Over long time scales, higher CO_2 concentrations decrease stomatal density and aperture, both of which reduce transpiration (Franks and Beerling 2009; Prentice and Harrison 2009). Observational and experimental studies confirm long-term and large-scale changes in leaf stomatal conductance in response to elevated CO_2 (Lammertsma et al. 2011; Warren et al. 2011). As leaf stomatal conductance decreases, ecosystem ET can also decline; however, any decline depends on stand age, species composition, and leaf area. Empirical studies linking reduced stomatal conductance to reduced stand-level ET have not yet been possible, and most researchers have used modeling to make this linkage.

Warren et al. (2011) applied the Forest BGC model to data from several elevated CO_2 studies and projected that ET was reduced by 11 % in older stands that did not experience an increase in leaf area. In younger stands, ET increased because of stimulation of leaf area, although field studies have not yet identified an increase in stand leaf area with elevated CO_2 (Norby and Zak 2011). In a modeling study of deciduous forests in the northeastern United States, the projected effect of elevated CO_2 on ET was modest, ranging from a 4 % decrease to an 11 % increase (Ollinger et al. 2008). In Mediterranean forest systems, changes in ET are also expected to be modest with increased temperature and CO_2, ranging from no change to a 10 % decrease (Tague et al. 2009). Although the effects of elevated CO_2 on ET remain uncertain, the direct effects will likely be modest (±10 %) compared to changes expected for other variables that affect ET, such as precipitation variability (Leuzinger and Körner 2010).

Higher temperature and thus increased vapor pressure deficit (VPD) between the inside of the leaf and the surrounding air may offset the water use efficiency effects of elevated CO_2. As the air becomes drier, transpiration typically increases following an exponential saturation curve, with the rate of increase continually slowed by reduced stomatal opening. Most studies show that a physiological effect of reduced stomatal conductance in response to elevated CO_2 is observed only when the canopy air is very humid (low VPD). In a study of six deciduous tree species, elevated CO_2 reduced transpiration by 22 %, but only at low VPD (Cech et al. 2003). These results suggest that the physiological effects of elevated CO_2 on ecosystem water balance may depend on precipitation and atmospheric humidity.

Warming has changed the timing of foliage green-up and senescence, but the effects of these phenological changes on ET are complex and poorly understood. Warming-induced lengthening of the growth season could increase ET and offset the reduction in stomatal conductance from elevated CO_2, but these effects are difficult to generalize across species and regions (Hänninen and Tanino 2011). The frost-free season across the United States has lengthened by about 2 weeks, resulting in a longer, warmer growing season, however, growth cessation in autumn might come earlier with increasing temperatures for some boreal and temperate tree species (Kunkel et al. 2004). For other tree species, spring budburst might be delayed by warmer temperatures (Zhang et al. 2007), perhaps because of insufficient chilling hours (Schwartz and Hanes 2010). In higher latitudes where chilling requirements are still being met, green-up is occurring sooner. Thus, springtime ET in the lower latitudes could be delayed, whereas ET in the higher latitudes could be advanced.

The potential increase in ET owing to a lengthened growing season can be constrained by water availability and drought in the growing season (Zhao and Running 2010). Water directly limits ET (lower water availability reduces transpiration), and many regions of the United States have experienced more frequent precipitation extremes, including droughts, over the last 50 years (Easterling et al. 2000b; Groisman et al. 2004; Huntington 2006; Solomon et al. 2007).

3.3.3 Changing Species Composition

Evapotranspiration is affected by the plant and tree species that comprise the canopy cover of a forest ecosystem. In general, pine forests are more responsive to climatic variation than are deciduous forests (Stoy et al. 2006; Ford et al. 2011); however, even within the same forest, growing-season transpiration rates among canopy species (adjusted for differences in tree size) can vary by as much as fourfold, and co-occurring species can differ considerably in their responsiveness to climatic variation (Ford et al. 2011). Characteristics of the xylem and sapwood, which vary by species, are among the most important determinants of stand transpiration in both observational (Vose and Ford 2011; Wullschleger et al. 2001) and theoretical studies (Enquist et al. 1998; Meinzer et al. 2005). Therefore, shifts in hydroclimate may be accommodated by changes in canopy leaf area, phenology, or species-based hydraulic efficiency.

Increased drought severity and frequency may contribute to changes in forest species composition in two ways. First, drought plays an important role in tree mortality (Allen et al. 2010); as soil water availability declines, forest trees either reduce stomatal conductance to reduce water loss (drought avoidance), or they experience progressive hydraulic failure (Anderegg et al. 2011) and eventually die. Second, some native insect outbreaks, and the mortality they cause, are also triggered by drought. Third, as temperature increases, plant metabolism increases exponentially, and if high temperature coincides with drought stress in forests, C starvation and mortality can occur quickly (Adams et al. 2009). For example, Adams et al. (2009) projected a fivefold increase in pinyon pine (*Pinus edulis* Engelm.) mortality from an increase of 4.3 °C, based on historical drought frequency. If drought frequency increases as expected, the projected mortality could be even higher.

Insect outbreaks and fire will be the likely primary forces behind rapid changes in forest composition and structure, although direct studies of these effects on hydrology are limited (Tchakerian and Couslon 2011). Potential biogeophysical effects from tree-killing biotic disturbances include (1) increased surface albedo, which will reduce the absorption of solar radiation, (2) decreased transpiration until the new forest is reestablished, and (3) decreased surface roughness, which affects atmospheric drag (Bonan 2008). After disturbances that cause widespread tree mortality, streamflow increases, the annual hydrograph advances, and low flows increase; at the same time, snow accumulation increases and snowmelt is more rapid after needle drop (Boon 2012; Pugh and Small 2011). Collectively, these studies show strong, but mostly indirect evidence that large-scale forest mortality will alter water cycling processes; however, the magnitude and duration of responses will differ among species and across regions.

3.3.4 Snowmelt

As a result of a warming climate, snow cover in North America has decreased in duration, extent, and depth over the last few decades, with increased interannual variability (Mote et al. 2005; Pagano and Garen 2005; Regonda et al. 2005; Barnett et al. 2008; Luce and Holden 2009). Reduced snowpack depth, persistence, and duration affect water stress, disturbance, erosion, and biogeochemical cycling in forest ecosystems. In arid and semiarid forests, early and reduced snowmelt leads to increased water stress in the late growing season, increased fire frequency, and higher susceptibility to insect attack (Breshears et al. 2005; Adams et al. 2012; Holden et al. 2011; Westerling et al. 2011). The rapid flush of water to the soil in spring snowmelt can release solutes that have been slowly accumulating as a result of subnival biogeochemical cycling (Williams et al. 2009). These spring pulses can provide the major input of nutrients to aquatic ecosystems. Reductions in the spring flush, and increased rain in winter and early spring, can change the timing of N release from northern forests. Higher frequency and magnitude of rain-on-snow events may also increase soil erosion, sedimentation, and landslides.

3.3.5 Soil Infiltration

Forest ecosystems typically support high infiltration capacities because of large soil pores developed by root systems and soil fauna, so surface runoff is uncommon. However, high-intensity precipitation or snowmelt events can rapidly move water in the soil to the unsaturated zone or groundwater, or into a local stream, particularly in steep terrain (Troch et al. 2009; Brooks et al. 2011). Increased storm intensity projected for the future may increase peak streamflow and flooding through this process.

3.3.6 Carbon and Water Tradeoffs

Expanding C sequestration or wood-based bioenergy markets to offset fossil fuel emissions may affect water resources (Jackson et al. 2005), depending on the specific management activity and scale of implementation. Planting fast-growing species for bioenergy production (or C sequestration) may reduce water availability (Jackson et al. 2005), but these reductions may be minor if the planting area is small relative to the watershed size. In wetter regions, where interception represents a higher proportion of ET, evergreen species may have a bigger effect on site water balance. In drier regions, where transpiration represents the greatest proportion of ET, species that use large amounts of water, such as *Populus* or *Eucalyptus*, would have a larger effect on the hydrologic cycle (Farley et al. 2005). Shortening rotation length might increase streamflow because the proportion of time during which the stand is at canopy closure (when leaf area index is highest and streamflow is lowest) will be reduced. In a global analysis of forest plantations, Jackson et al. (2005)

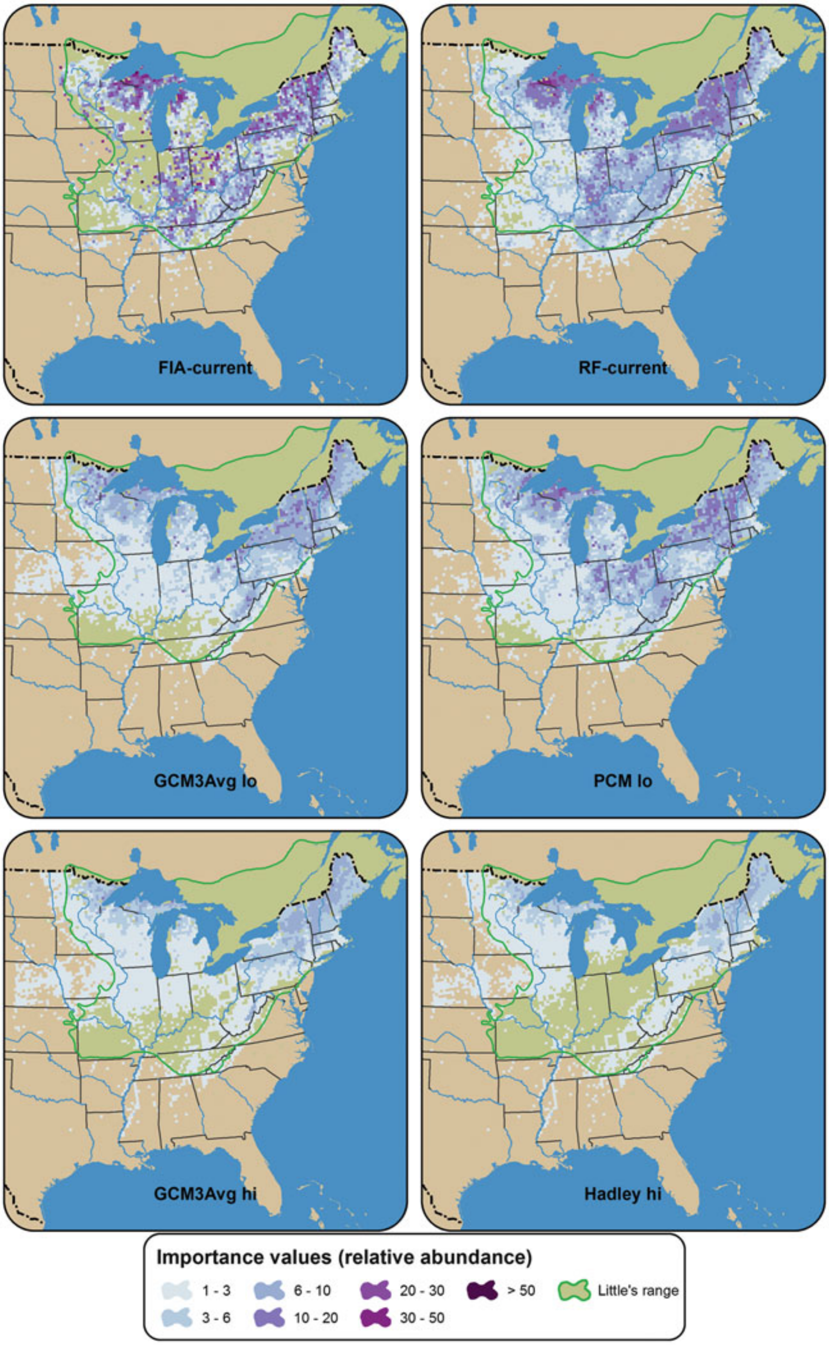
found the biggest reductions in streamflow in plantations that were 15–20 years old. This would be exacerbated if short-rotation forests are irrigated, which might be considered a necessity in some areas of the western United States where drought frequency and intensity are expected to increase.

3.4 Tree Species Distribution

The ranges of plant and animal species have always shifted through time (e.g., Davis and Shaw 2001), but in recent decades, some species may be moving faster than in the past (Parmesan and Yohe 2003; Chen et al. 2010; Dobrowski et al. 2011). For example, in a meta-analysis of 764 species range changes (mostly insects and no tree species), the average rate of northward migration was 16.9 km per decade (Chen et al. 2011). In contrast, an earlier meta-analysis, using 99 species of birds, butterflies, and alpine herbs, reported a northward migration of 6.1 km per decade (Parmesan and Yohe 2003). There is also evidence of upward elevation migration of tree species (Beckage et al. 2008; Holzinger et al. 2008; Lenoir et al. 2008).

Woodall et al. (2009) used forest inventory data to investigate surrogates for migration among 40 tree species in the eastern United States, comparing mean latitude of biomass of larger trees (>2.5 cm diameter) relative to mean latitude of seedling density (<2.5 cm diameter) across each species range of latitude. For many species, this analysis indicated higher regeneration success at the northern edge of their ranges. Compared to mean latitude of tree biomass, mean latitude of seedlings was significantly farther north (>20 km) for the northern study species, southern species showed no shift, and general species showed southern expansion. Density of seedlings relative to tree biomass of northern tree species was nearly ten times higher in northern latitudes than in southern latitudes. These results suggest that Eastern tree species have moved northward, with rates approaching 100 km per century for some species. Pollen records suggest migration rates for tree species during the Holocene were 2–2.5 km per decade (Davis 1989), a time when species were not slowed by forest fragmentation (Iverson et al. 2004a, b).

Vegetation change can be projected for the future using two types of predictive models: (1) empirical, species distribution models that establish statistical relationships between species or life forms and (often numerous) predictor variables, and (2) process-based models, which simulate vegetation dynamics at the taxonomic resolution of species or life forms. There are well-recognized tradeoffs between using these different models to assess potential changes in species habitats resulting from projections of environmental change (Thuiller et al. 2008). When both approaches yield similar results for a particular area, confidence in model projections is improved. Demographic studies inform species distribution models (SDMs), and migration models are sometimes incorporated in process-based models.


FIA-current
RF-current
GCM3Avg lo
PCM lo
GCM3Avg hi
Hadley hi
Importance values (relative abundance)
1 - 3
3 - 6
6 - 10
10 - 20
20 - 30
30 - 50
> 50
Little's range

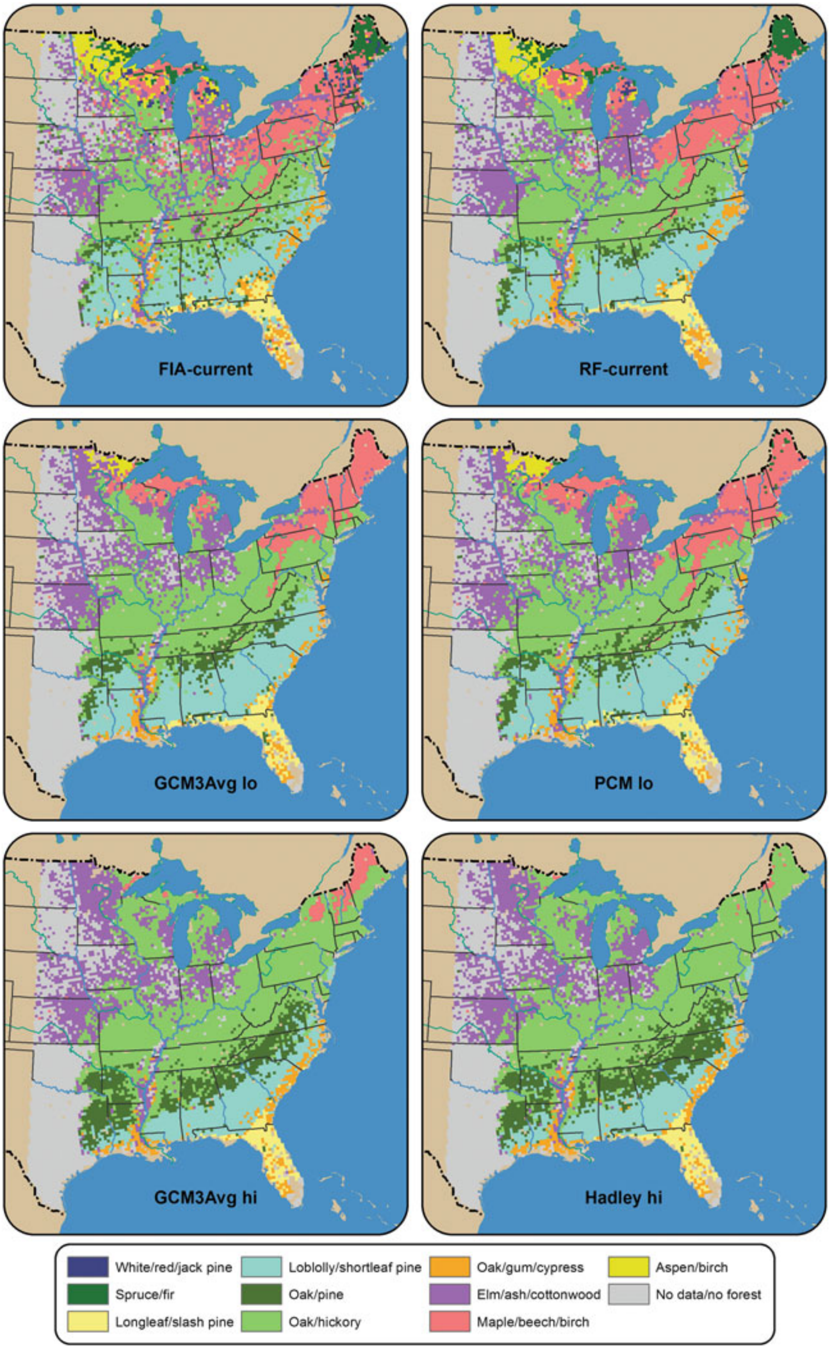
3.4.1 Modeling Species Distribution and Abundance

3.4.1.1 Species Distribution Models

Species distribution models, which extrapolate species distributions in space and time, are based on statistical models of habitat suitability (Franklin 2009) and built with observations of species occurrences along with environmental variables thought to influence habitat suitability and "equilibrium" species distribution. Predictive mapping of suitable habitat (but not whether a species will reach those habitats) in space and time are therefore possible. The SDMs have limitations, including assumptions that (1) selected variables reflect the niche requirements of a species, (2) species are in equilibrium with their suitable habitat, (3) species will be able to disperse to their suitable locations, (3) projections can be made for novel climates and land covers, (4) effects of adaptation and evolution are minimal, and (5) the effects of biotic interactions (including human interactions) are minimal (Ibáñez et al. 2006; Pearson et al. 2006). However, SDMs can provide glimpses of probable futures useful for incorporating future conditions into conservation and management practices.

Species distribution models project a northward movement of tree species habitat in North America from 400 to 800 km by 2100 depending on the assumptions used in projecting future climate (Iverson et al. 2008; McKenney et al. 2011). Species distribution model projections also differ based on future scenarios and with time. For example, under a scenario of high greenhouse gas emissions (Hadley A1F1), about 66 species would gain and 54 species would lose at least 10 % of their suitable habitat under climate change. A lower emission pathway would result in both fewer losers and gainers. Sugar maple (*Acer saccharum* Marsh.) would lose a large proportion of its habitat under the warmest scenario (Lovett and Mitchell 2004; Iverson et al. 2008) (Fig. 3.2), but would still maintain a presence of habitat in most areas. When multiple species are compiled to create "forest types," models project a loss of suitable habitat for spruce-fir (*Picea-Abies*), white-red-jack pine (*Pinus strobus* L., *P. resinosa* Aiton, *P. banksiana* Lamb.), and aspen-birch (*Populus-Betula*), but an expansion of suitable habitat for oak-hickory (*Quercus-Carya*) (Iverson and Prasad 2001; Iverson et al. 2008) (Fig. 3.3).

Fig. 3.2 Maps of current and potential future suitable habitat for sugar maple in the United States show potential northward movement of habitat by 2100. In addition to showing the range of sugar maple in Little (1971), the map includes the current inventory estimate of abundance from U.S. Forest Service Forest Inventory and Analysis (FIA-current) sampling and the modeled current distribution (RF-current). Model projections for future climate are: (1) low emission scenario (B1) using the average of three global climate models (GCM3 Avg lo), (2) low emission scenario (B1) using the National Center for Atmospheric Research Parallel Climate Model (PCM lo), (3) high emission scenario (A1F1) using the average of three global climate models (GCM3 Avg hi), (4) high emission scenario (A1F1) using the HadleyCM3 model (Hadley hi) (Data from Prasad and Iverson (1999-ongoing))


FIA-current
RF-current
GCM3Avg lo
PCM lo
GCM3Avg hi
Hadley hi
White/red/jack pine
Spruce/fir
Longleaf/slash pine
Loblolly/shortleaf pine
Oak/pine
Oak/hickory
Oak/gum/cypress
Elm/ash/cottonwood
Maple/beech/birch
Aspen/birch
No data/no forest

3.4.1.2 Process Models

To model species composition changes, a fully process-driven approach might be preferable to isolate mechanisms and to create "what-if" scenarios. However, such an approach is presently difficult because of the (1) necessity of detailed parameterization of species life histories and physiologies for a large number of species, (2) complexity of many interacting disturbance factors, and (3) necessary high-resolution modeling over very large areas (Lawler et al. 2006). Dynamic global vegetation models (DGVM) operate at scales from regional (hundreds of kilometers) to global; these models can aggregate species into life forms or plant functional types (PFTs), using structural or functional attributes such as needleleaf vs. broadleaf and evergreen vs. deciduous (Bachelet et al. 2003; Bonan et al. 2003; Neilson et al. 2005). Most of these models project shifts to more drought-tolerant and disturbance-tolerant species or PFTs for future climates. This general shift in vegetation may be offset by physiological changes induced by CO_2 fertilization, as suggested by a DGVM (MC1) that links water-use efficiency to CO_2-simulated expansion of forests into areas whose climate is currently too dry (Bachelet et al. 2003). This particular issue deserves further study to resolve the extent and duration of such mitigating effects of CO_2; these effects could change substantially depending on the outcome of climate change projections.

Ravenscroft et al. (2010) used the LANDIS model to simulate the potential effects of climate change to 2095 and found that mesic birch–aspen–spruce–fir and jack pine–black spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb.) forest types would be substantially altered because of the loss of northerly species and the expansion of red maple (*Acer rubrum* L.) and sugar maple. Another promising modeling system that also includes climate variables is the Regional Hydro-Ecologic Simulation System (RHESSys) (Tague and Band 2004). Using this model in a Sierra Nevada mountain system, Christensen et al. (2008) found significant elevation differences in vegetation water use and sensitivity to climate, both of which will probably be critical to controlling responses and vulnerability of similar ecosystems under climate change. Transpiration at the lowest elevations was consistent across years because of topographically controlled high moistures, mid-elevation transpiration rates were controlled primarily by precipitation, and high-elevation transpiration rates were controlled primarily by temperature (Fig. 3.4).

◄

Fig. 3.3 Maps of current and potential future suitable habitat for U.S. Forest Service forest types (named according to dominant species) in the eastern United States show potential northward movement of forest types by 2100. The map includes the current inventory estimate of abundance from U.S. Forest Service Forest Inventory and Analysis (FIA-current) sampling and modeled current distribution (RF-current). Model projections for future climate are: (1) low emission scenario (B1) using the average of three global climate models (GCM3 Avg lo), (2) low emission scenario (B1) using the National Center for Atmospheric Research Parallel Climate Model (PCM lo), (3) high emission scenario (A1F1) using the average of three global climate models (GCM3 Avg hi), (4) high emission scenario (A1F1) using the HadleyCM3 model (Hadley hi) (From Iverson et al. 2008)

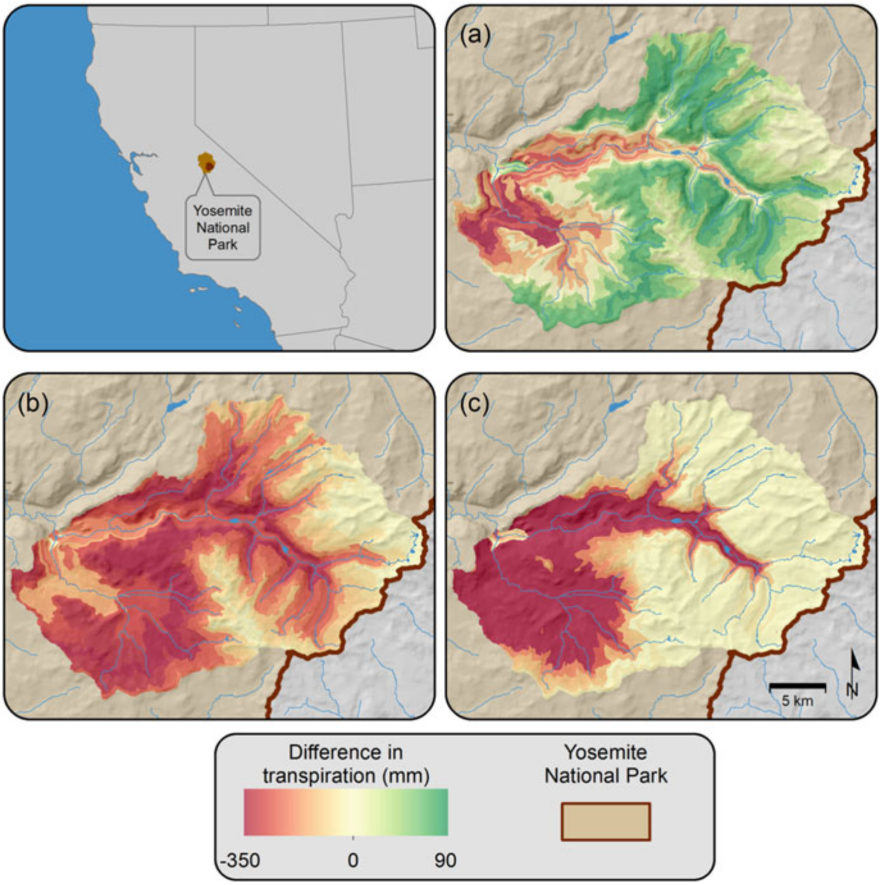


Fig. 3.4 Maps of Upper Merced River watershed, Yosemite Valley, California, showing areas with differences in transpiration in (**a**) warmest vs. coldest simulation years, (**b**) wet vs. average precipitation year, and (**c**) dry vs. average precipitation year. The largest decreases in transpiration between years are shown in *red*; increases between years are shown in *green* (From Christensen et al. 2008, with permission)

3.4.1.3 Demographic Studies

Demographic studies track individuals over time, rather than using periodic plot-level inventories, to fully understand the role of climate relative to other factors like competition, variation in physiology and function, and vulnerability to insects and pathogens. Demographic data sets are rare, but one study has tracked more than 27,000 individuals of 40 species over 6–11 years to address these interactions over a portion of the southeastern United States (Clark et al. 2011). This study found that the primary climatic controls are spring temperature (regulating species fecundity) and growing season moisture, particularly for species of *Pinus*, *Ulmus*, *Magnolia*, and *Fagus*. Pitch pine (*Pinus rigida* Mill.) tracked both spring temperature and summer drought, yellow poplar (*Liriodendron tulipifera* L.) tracked neither, and sweetgum (*Liquidambar styraciflua* L.) tracked summer drought but not spring temperature (Clark et al. 2011). Overall, the effect of competition on growth and mortality exceeded the effects of climatic variation for most species. Thus, demographic tracking can determine the vulnerability of individual trees to various factors, including climate change over time, variation in abiotic variables over space, and competition (Clark et al. 2011).

3.4.1.4 Dispersal and Migration Models

Each species affected by climate change will need to either migrate or be moved to a suitable habitat. Approaches used to model migration include reaction–diffusion models, phenomenological models, mechanistic models, and simulation models (Clark et al. 2003; Hardy 2005; Katul et al. 2005; Nathan et al. 2011). Recent advances in digital computation and more reliable data from seed dispersal studies have improved these models so that they can project the parameter values of seed dispersal curves as well as seed distributions. For example, Nathan et al. (2011) modeled 12 North American wind-dispersed tree species for current and projected future spread according to 10 key dispersal, demographic, and environmental factors affecting population spread. They found a low likelihood for any of the 12 species to spread 300–500 m per year, the rate of change that may be required under climate change (Loarie et al. 2009). The SHIFT model uses historical migration rates along with the strengths of the seed sources (abundance within the current range) and potential future sinks (abundance of potential suitable habitat). When model outputs of colonization potentials were combined with an SDM (DISTRIB) simulation of suitable habitat for five species—common persimmon (*Diospyros virginiana* L.), sweetgum, sourwood (*Oxydendrum arboreum* [L.] DC), loblolly pine, and southern red oak (*Quercus falcata* Michx.)—only 15 % of the newly suitable habitat had any likelihood of being colonized by those species within 100 years (Iverson et al. 2004a, b). These results suggest that a substantial lag will occur before species migrate into the new suitable habitat.

3.4.2 Assisted Migration

As noted above, models suggest that many tree species will be unable to migrate to suitable habitat within 100 years (Iverson et al. 2004a, b) and may face serious consequences if they cannot adapt to new climatic conditions. Assisted migration may help mitigate climate change by intentionally moving species to climatically suitable locations outside their natural range (McLachlan et al. 2007; Hoegh-Guldberg et al. 2008). Assisted migration has been controversial, with some advocating for it (Minteer and Collins 2010; Vitt et al. 2010) and some against

(Ricciardi and Simberloff 2009). Proponents state that these drastic measures are needed to save certain species that cannot adapt or disperse fast enough in response to rapid climate change. The main concern of opponents is that the placement of species outside their range may disturb native species and ecosystems when these "climate refugees" establish themselves in new environments. The uncertainty of climate in the future and the complexity and interactions associated with ecosystem response also argue against assisted migration.

One way to resolve the debate is to subdivide assisted migration into "rescue-assisted migration" and "forestry-assisted migration." Rescue-assisted migration moves species to minimize the risk of extinction and local extirpation in the face of climate change, and is the source of most of the controversy. Forestry-assisted migration is aimed more at maintaining high levels of productivity and diversity in widespread tree species that are commercially, socially, culturally, or ecologically valuable (Gray et al. 2011; Kreyling et al. 2011). Maintaining forest productivity and ecosystem services is generally the focus of forestry-assisted migration. Given the broad distribution of most tree species, and the relatively short distances proposed for tree seed migration, forestry-assisted migration typically involves transfers within or just beyond current range limits to locations where a population's bioclimatic envelope is expected to reside within the lifetime of the planted population (Gray et al. 2011). The introduction of genotypes to climatically appropriate locations may also contribute to overall forest health by establishing vigorous plantations across the landscape that are less susceptible to forest pests and pathogens (Wu et al. 2005). This approach may contribute to the continued flow of ecosystem services such as wildlife habitat, erosion prevention, and C uptake (Kreyling et al. 2011). If practiced in a manner in which genotypes are transferred within or just beyond current range limits, forestry-assisted migration may be a viable tool for adaptation to climate change, especially if limited to current intensively managed plantations.

3.5 Effects of Altered Forest Processes and Functions on Ecosystem Services

Ecosystem services link the effects of altered forest processes, conditions, and disturbance regimes to human well-being (World Resources Institute 2005). A broad range of utility and values derive from four broad types of ecosystem services: (1) provisioning or products from ecosystems, (2) regulation of ecosystem processes, (3) cultural or nonmaterial benefits, and (4) supporting services required for the production of all other ecosystem services (Joyce et al. 2008) (Fig. 3.5). Anticipated climate changes portend changes in all types of ecosystem services derived from forests. Because the assessment endpoint for ecosystem services is human well-being, we are ultimately concerned about the potential effects of climate change on the ecosystem services that forests provide.

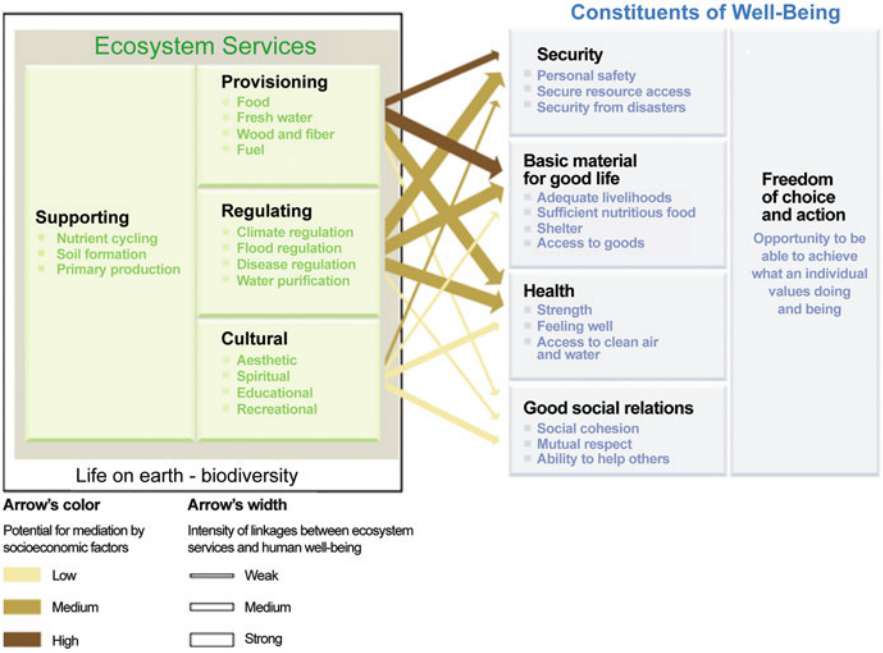


Fig. 3.5 Linkages between ecosystem services and human well-being (From World Resources Institute 2005)

Ecosystem services differ across temporal and spatial scales but are most often assessed and recognized at large spatial scales. Disturbances (natural and human) and stressors can control delivery of ecosystem services across variable timeframes. Ecosystem services occur in forests not as a single service but rather as a bundle of services. The bundle of services changes with time and in response to disturbance regimes and stressors. Vulnerability of ecosystem services to climate change will vary widely, depending not only on the service of concern (e.g., wood products or flood regulation) and location (defined by region), but also on the location in reference to human condition, such as rural versus urban settings. The value of the affected service multiplied by the likelihood of effect defines the risk to ecosystem services and provides a framework for understanding potential consequences and prioritizing actions.

Climate-related mechanisms of change in U.S. forests could alter ecosystem services in ways that are not yet fully understood, and estimating these effects introduces another layer of uncertainty. That is, climate regulates forest processes that control future forest conditions that determine future ecosystem services. Still, the potential effects of climate change on forest ecosystems could have profound and mostly disruptive consequences for ecosystem services with important implications for human well-being. Ecosystem services also depend on interactions with land use, human demographics, and economies, which may simultaneously adjust to climatic stimuli (see Chap. 5).

Forests in the United States consist of both managed (active) and unmanaged (passive) ecosystems (Ryan et al. 2008) held in public and private ownerships. Some public forests or wildlands are withdrawn from active management (e.g., national parks, state parks, wilderness areas, wild and scenic rivers), but most lands are managed for multiple-use goals (e.g., most national forests and Bureau of Land Management lands). Public land management in the United States is largely focused on non-market ecosystem services, including recreation, aesthetic values, and water quality. Most forest management for timber production occurs on private forest lands, using both capital-intensive (short rotation plantation silviculture) and land-extensive approaches (occasional harvesting followed by natural regeneration). Private lands also provide the full spectrum of ecosystem services, either by design through conservation easements, or as a byproduct of other management objectives (Butler et al. 2007). In many cases, private forest lands provide ecosystem services that accrue to broader social well-being without equitable financial compensation.

Ecosystem services provided under current climatic conditions differ across the assortment of public and private forests that are managed actively or passively. As a consequence of the regional distribution of anticipated future climate change, the provision of ecosystem services from these lands could also change and be modified by mitigation and adaptation strategies (see Chaps. 7 and 8). Social perception of risks to ecosystem services will be determined by the rate of change in these services (flows) (see Chap. 9), as well as by an understanding of mitigation and adaption strategies applied in response to climate change. Social systems will adapt to climate change and affect the condition of forests in the United States and throughout the world.

Several mechanisms of change in forest ecosystems have implications for ecosystem services. First, climate change could alter the amount and distribution of forest biomass in forests, either through shifts in productivity associated with atmospheric C concentrations or through altered forest disturbance regimes. Changes in forest biomass directly influence the supply of all wood products from lumber to fuel for electricity production (provisioning services), and they alter the amount of C stored in forest pools (a regulating service) (see Chap. 7). Future productivity and disturbance effects would probably be focused in the Rocky Mountain and intermountain West and Alaska, where only a small portion of U.S. timber production occurs. Declines in timber production would be small in the context of national markets, but they could represent substantial shares of local rural economic activity.

Changes in tree cover will affect microclimatic conditions (e.g., the cooling of urban heat islands), whereas shifts in C stocks through accumulation of biomass could affect changes in global climate trajectories. Projections of accelerated emissions related to elevated insect epidemics and fire activity in the Rocky Mountains and southwestern United States could represent a substantial effect on forest C storage, potentially shifting U.S. forests from net C sinks to net C emitters (Wear et al. 2012) (see Sect. 3.2 and Chap. 7).

The effects of climate change on forest productivity differ by region and contain sufficient uncertainty that their influence on timber markets and C stocks are difficult to project. However, if forest productivity were to increase in the eastern United States and decrease in the western United States (see Sect. 3.2), this could accelerate the shift in timber production from West to East, and especially to the Southeast.

Estimates of the economic consequences of insect and pathogen outbreaks focus on timber market effects (e.g., southern pine beetle [*Dendroctonus frontalis* Zimmerman] (Pye et al. 2011)) or the influence of tree mortality on property values (e.g., hemlock woolly adelgid (Holmes et al. 2010)). These measures of market effects for price-based services address one element of a complex of values affected by forest disturbances. In the case of forest insects, management decisions already account for a certain level of expected tree mortality, so the more relevant question is whether effects significantly exceed the “background” losses associated with endemic insects and pathogens. Property values define the effect of disturbance and related mortality on ecosystem services delivered to private property owners, but they cannot capture the “public good” aspects of changes to forest aesthetics for people who view forests. To illustrate, widespread tree mortality related to pine beetle epidemics on national forests can reduce the aesthetic values for millions of people. These “quality of life” effects represent real value losses, but they are difficult to quantify and may be transitory as regrowth occurs and society adjusts expectations regarding what constitutes a natural or aesthetically appealing condition.

Climate change could alter the complex of interactions between forest conditions and water flow and quality. Forest cover and condition constitute only one element of a complex system, so effects may be difficult to isolate, but forest condition appears to be strongly related to flood protection (a regulating service) and water quantity and quality (a provisioning service). More variable precipitation patterns (stronger drought and extreme rainfall events) increase the service value of forests in protecting against flooding and landslides, but they also change forest conditions in ways that reduce soil-protecting qualities. This negative feedback suggests potential for accelerated losses of flood protection services of forests. Reduced supplies of these services would coincide with strong growth in the demand for water services caused by population growth and associated water needs for personal and commercial uses.

The longer term and less certain effects of climate change on forest conditions discussed above suggest more forests in a state of disequilibrium with new species-climate associations. The notion of “novel” conditions suggests “unknowable” implications, especially regarding the supply and demand for ecosystem services and the reactions of private landowners and government to increasing scarcity of important services. However, economic factors will likely drive responses, and the risks of climate change to forests may open public dialogue regarding the costs and benefits of providing ecosystem services. Changes in forest policy may be needed to align producers and consumers of services on private and public forest lands (e.g., providing compensation for private landowners’ provision of scarce ecosystem services).

Adaptation strategies in forests can build resistance to climate-related stressors, increase ecosystem resilience by minimizing the severity of climate change effects, or facilitate large-scale ecological transitions in response to changing environmental conditions (see Chap. 8). Adaptation and mitigation strategies for forests can alter the supply of ecosystem services and involve explicit tradeoffs between services. For example, thinning and fuel treatment to reduce the vulnerability of forests to disturbance regimes and stressors defines a specific tradeoff between short-term changes in C stocks and long-term stability of C emissions. Resistance, resilience, and transitions of forest ecosystems to new conditions are tiered to increasing levels of environmental change and time scales, and each adaptation strategy will result in a different bundle of ecosystem services.

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