

Responses of Temperate Forest Productivity to Insect and Pathogen Disturbances

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biological forcing, carbon, CO₂, climate change, disturbance, ecosystem, net primary production, succession, temperature

Abstract

Pest and pathogen disturbances are ubiquitous across forest ecosystems, impacting their species composition, structure, and function. Whereas severe abiotic disturbances (e.g., clear-cutting and fire) largely reset successional trajectories, pest and pathogen disturbances cause diffuse mortality, driving forests into nonanalogous system states. Biotic perturbations that disrupt forest carbon dynamics either reduce or enhance net primary production (NPP) and carbon storage, depending on pathogen type. Relative to defoliators, wood borers and invasive pests have the largest negative impact on NPP and the longest recovery time. Forest diversity is an important contributing factor to productivity: NPP is neutral, marginally enhanced, or reduced in high-diversity stands in which a small portion of the canopy is affected (temperate deciduous or mixed forests) but very negative in low-diversity stands in which a large portion of the canopy is affected (western US forests). Pests and pathogens reduce forest structural and functional redundancy, affecting their resilience to future climate change or new outbreaks. Therefore, pests and pathogens can be considered biotic forcing agents capable of causing consequences of similar magnitude to climate forcing factors.

Contents

INTRODUCTION	548
A Historical Perspective on Forest Succession and Disturbance	549
Climate Versus Biological Forcing Factors of Forest Productivity	553
BIOTIC FORCING FACTORS AND THEIR IMPACTS ON FOREST	
ECOSYSTEM DYNAMICS	555
Mountain Pine Beetle (Native)	555
Spruce Budworm (Native)	556
Forest Tent Caterpillar (Native)	556
Emerald Ash Borer (Nonnative)	556
Gypsy Moth (Nonnative)	557
Beech Bark Disease (Nonnative)	557
Dutch Elm Disease (Nonnative)	557
ASSESSING THE IMPACTS OF FOREST PESTS ON	
FOREST CARBON DYNAMICS	557
Do Pests and Pathogens Have Differential Impacts	
or Legacies on Forest Carbon Cycling?	558
To What Degree Does Disturbance Severity Impact Forest Carbon Cycling?	558
INTERACTIONS BETWEEN CLIMATE CHANGE AND FOREST	
PESTS AND PATHOGENS	559
CONCLUSION	561

INTRODUCTION

Net primary production (NPP): the total amount of gross primary production allocated to production of new biomass after accounting for plant respiratory losses (i.e., the difference between gross primary production and autotrophic respiration)

Net ecosystem production (NEP): the C accumulation by ecosystems (i.e., the difference between gross primary production and total ecosystem respiration)

Forest ecosystems blanket more than 30% of the terrestrial biosphere, and via the processes of photosynthesis and respiration, they exchange considerable quantities of CO₂ with the atmosphere (40). The strength of these competing fluxes indicates C uptake or loss and is partly a function of the efficiency by which photosynthesis is converted into net biomass gains (e.g., carbon use efficiency) (27, 81, 152). At the ecosystem level, these biomass gains contribute to net primary production (NPP) and net ecosystem production (NEP). Because of consistently high positive rates of NPP and NEP over millennia, forests constitute one of the largest terrestrial C reservoirs and sinks, accumulating considerable quantities of C in above- and belowground biomass and soils (106, 110).

As C sinks, forests help buffer the anthropogenic increase of CO₂ in the atmosphere, which has been accumulating throughout the Holocene (63, 123). However, their ability to provide consistent atmospheric CO₂ buffering is uncertain because drivers such as steadily rising atmospheric CO₂ concentrations (63), forest fires (147), shifts in forest cover (48, 95), climate change (25), and the increased prevalence of pest and pathogen outbreaks affect the function and structure of forest ecosystems, impacting their NPP and NEP (62) (**Figure 1**). Considerable progress has been made in understanding the mechanisms that govern forest C storage following abiotic (e.g., climate, fire, and drought) and other severe disturbances (e.g., harvesting), yielding a wealth of knowledge about the relationships among disturbance severity, successional dynamics, and C storage (1, 12, 13, 15, 18, 23, 47, 70, 80, 136), but mechanisms that govern forest C storage following pest and pathogen outbreaks are less well known.

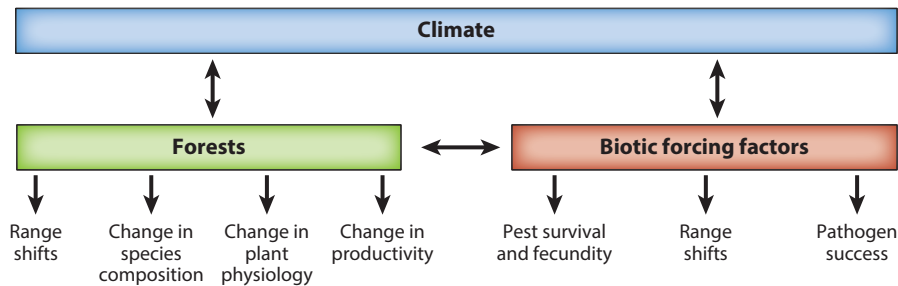


Figure 1

Interactions among climate, forests, and biotic forcing factors. Two-way arrows denote feedbacks; one-way arrows indicate how main effects may manifest change.

Despite the ubiquitous nature of pest and pathogen disturbances (**Figure 2**, **Table 1**, **Supplemental Table 1**; follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>), the paucity of information regarding forest responses requires that we derive our understanding of these events almost exclusively from severe stand-replacing disturbances. Forest disturbance and recovery are often defined within the ecological framework of the stage recovery phase (143), in which all species present after a disturbance compete to fill the niche created by a given disruption (see below). Disturbances caused by biological agents (e.g., pests and pathogens) effectively impair the competitive abilities of host species to participate in the succession and recovery processes. The complex relationships between forest succession and disturbance, climate forcing, biological agents, and associated feedbacks need to be considered more holistically to improve the predictive capabilities of present productivity and climate models (**Figure 1**). Furthermore, we need a better understanding of the human-climate-ecosystem interactions that trigger outbreaks and of the successional paths following disease-induced diffuse mortality in forests that determine emergent ecosystem structure as well as NPP and NEP trajectories. To help fill this void, we have reviewed the literature to explore how native and invasive pest and pathogen disturbances impact forest ecosystem properties and the C cycle in temperate regions.

Supplemental Material

Succession: the process of natural forest replacement of plants and species assemblages in an area over time

Forest disturbance: any biotic or abiotic factor that results in the interruption of ongoing succession or alters the state of forest ecosystems

Diffuse mortality: episodic tree death caused by drought or outbreaks that result in forest patches of dead individuals and/or in widespread single-tree mortality within the forest matrix

A Historical Perspective on Forest Succession and Disturbance

Because of the unique long life cycles of trees, forest ecosystems are routinely exposed to natural disturbances (e.g., pests, pathogens, fire, drought, windthrow, and tree fall). These disturbances are ubiquitous in nature and vary in frequency, severity, and magnitude. Forest disturbance types vary both regionally and across biomes; anthropogenic deforestation is most prominent in tropical forests, and forest fires, pest outbreaks, and silviculture are most common in temperate and boreal forests (118).

Multiple explanations have been proposed for the process of succession and community restructuring. Clements (21) adopted the views of contemporary Henry Cowles (24) and developed the Clementsian paradigm of succession, in which succession is an orderly, linear progression culminating in a climax community. Gleason (44–46) viewed communities as the result of interactions between individual species and the environment in combination with chance events. Assimilated from these viewpoints, the law of vegetation dynamics is a universal generalization that specifies three major factors driving vegetation dynamics: site availability, species availability,

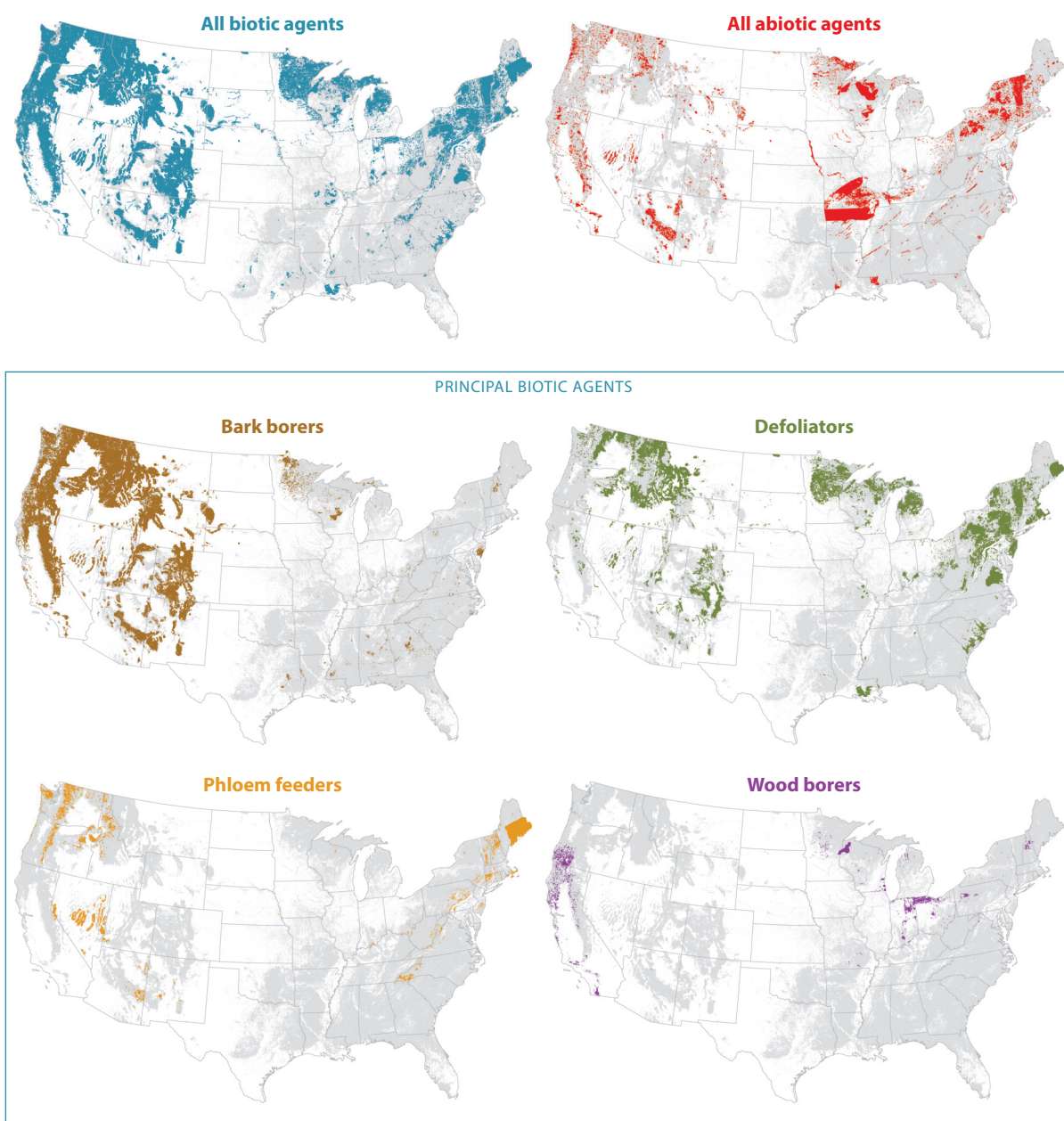



Figure 2

Geographic distribution of forests impacted by insect and disease in the United States. The top two maps compare biotic and abiotic impacts; the bottom maps show the principal biotic agents. Data are derived from the US Department of Agriculture Forest Service Aerial Detection Survey 2004–2013. The forested area (gray) shows the 2002–2003 forest type groups; the affected area represents approximately 15% of this area in the contiguous United States. Map projection: US Contiguous Albers Equal Area Conic, US Geological Survey version, North American Datum (NAD) 1983.

Table 1 Disturbance agents in the United States and area impacted from 2007 to 2012

Disturbance category	Area impacted (acres)
Defoliator	40,642,585.5
Bark borer	34,539,182.2
Abiotic	26,228,153.6
Phloem feeding	10,824,579.3
Other	7,654,295.8
Fungus	5,601,401.2
Complex	4,986,967.1
Growth decline	1,783,008.4
Wood borer	1,553,160.6
Anthropogenic	144,695.2
Parasitic plants	10,792.5
Invasive plants	221.9
Total (all agents)	116,193,814.0

Data derived from the US Department of Agriculture Forest Service Aerial Detection Survey 2004–2013. For a list of individual agents within each disturbance category, see **Supplemental Table 1**.

 **Supplemental Material**

and differential species performance (the law of dynamic tolerance) (112). Although monotonic change and stability need not be necessary in postdisturbance recovery, the law of vegetation dynamics implies nonfixed directionality, broadening the Clementsian paradigm (112). The theory of gap dynamics is complementary to these succession paradigms and suggests that tree-level disturbances that create small gaps can allow the persistence of shade-intolerant species within old-growth forests (see 151 and references therein). Finally, forest succession can be thought of as a highly despotic form of lottery competition in which many individuals vie for a position in the canopy; although the canopy will surely be filled, the probability of a particular individual actually reaching the canopy is slim. Within this framework, individuals remaining after a disturbance have the highest probability of reaching the canopy and as such will drive successional dynamics in new directions. Thus, disturbance frequency, severity, and magnitude drive succession via alterations to forest structure, composition, and biogeochemical cycling (112, 113, 124) (**Figure 3**).

Structural stages for abiotic forest disturbance recovery have been well defined and incorporated into ecosystem, biogeochemical, and vegetation dynamic models (31, 55, 96, 143). Following a major disturbance (e.g., fire, landslide, or clear-cut), spores, seed banks, seed rain, and existing seedlings and saplings provide the basis for regeneration during the stand initiation stage (111). As the new generation of tree species becomes established, light and resource competition limit the density of individuals. During this stem exclusion stage, tree mortality at the forest scale is thought to be dependent on increasing biomass/density of stems, which compete for light and nutrients, and on the mortality of shade-intolerant early successional species. During stand stem exclusion, the understory fills in, the forest canopy becomes reestablished, and maximum leaf area index (comparable to the size of the photosynthetic tissue and thus related to stand productivity and NPP) is attained, as are maximum soil C inputs (NEP), but a reduction in the leaf area-to-wood production ratio over time begins (leading to a decline in growth efficiency). Once canopy closure is reached, the understory reinitiation stage maintains positive levels of NPP and large inputs to forest floor and soil C from the mortality of large trees. Canopy complexity and diversity plateaus at the old-growth stage, and NPP continues to decline as dominant species reach maximum height. A new disturbance event at any stage of recovery is thought to follow similar dynamics of NPP and C flux (**Figure 3**).

Stem exclusion:

a process that occurs early in forest succession where high mortality rates occur in part because of competition for light and nutrients

Leaf area index:

a dimensionless quantity accounting for the one-sided area of leaf tissue (m²) per unit ground surface area (m²)

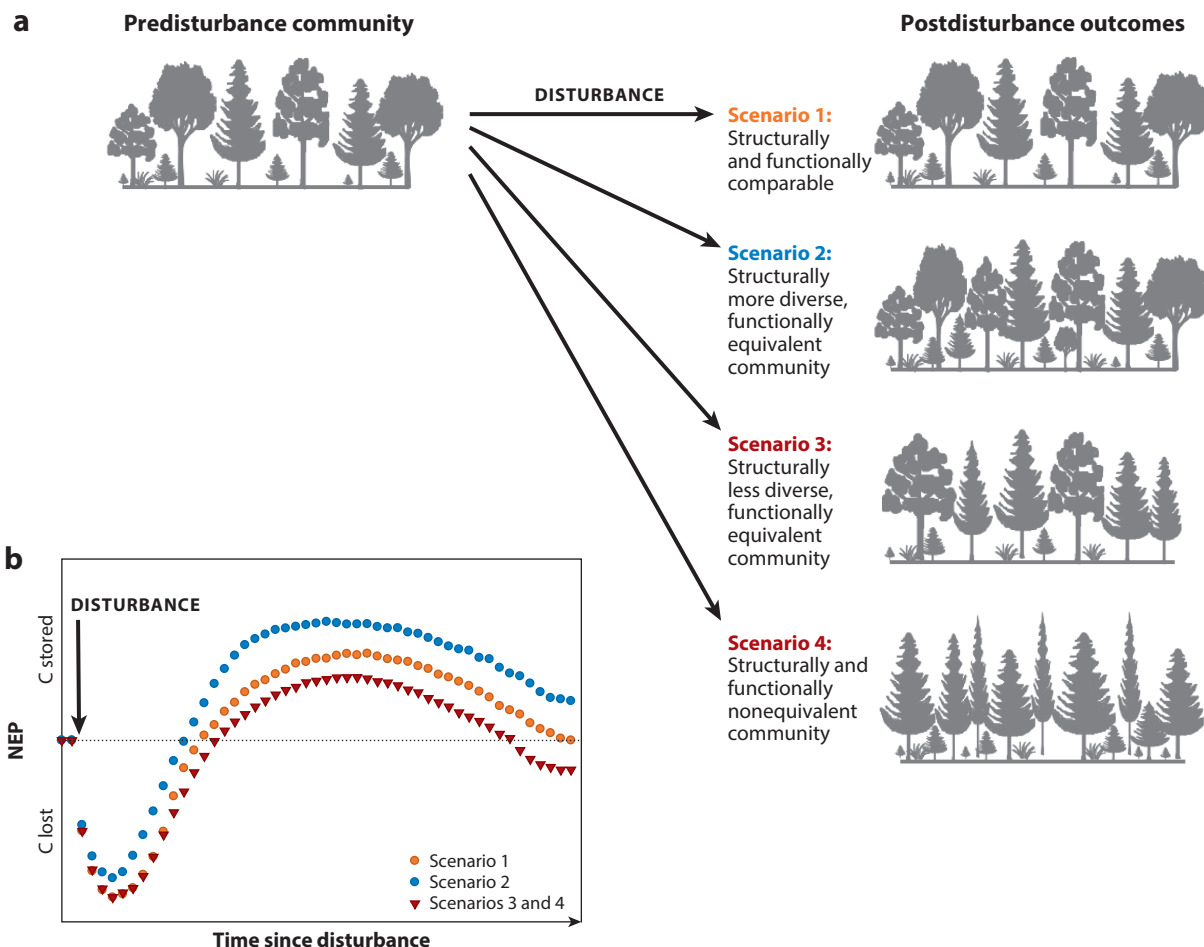


Figure 3

Ways in which forest structure, composition, and biotic drivers can shape forest ecosystems and their C dynamics. (a) An idealized forest in a predisturbance community (*left*) and four postdisturbance communities (*right*). The latter depict a community that is both structurally and functionally comparable to the predisturbance community (scenario 1), a community that is structurally more diverse and functionally equivalent (scenario 2), a community that is structurally less diverse and functionally equivalent (scenario 3), and a community that is structurally and functionally not equivalent (scenario 4). (b) The net ecosystem production (NEP) dynamics associated with each successional outcome.

An estimated two-thirds of the world's forests are in the disturbance recovery phase, and a substantial amount of forest land in the United States is now affected by biotic disturbance (Figure 2, Table 1). Forest disturbances modify canopy structure and alter forest dynamics, species composition, tree density, and the competitive landscape, leading to impacts on terrestrial C dynamics and their coupled interactions with the atmosphere (e.g., 41). The increase in the area of forests recovering from disturbance over the last few decades is accounting for a sustained increase in the sink capacity of forests, particularly in temperate regions (106). As mentioned above, during the recovery phase following moderate to severe disturbances caused by fire or harvest, leaf area increases and C uptake resumes, but with pests and pathogens, the successional trajectories may follow one of four scenarios (Figure 3).

First, the forest understory may comprise the same species as its overstory, and after a stem exclusion phase, it may reestablish a similar canopy and maintain previous rates of C uptake (**Figure 3a**, scenario 1). This scenario is unlikely to occur following recovery from pest or pathogen outbreaks if conditions for attack persist on the targeted species, as was the case with the chestnut blight (*Cryphonectria parasitica* Murr.) (2, 39). Second, because of targeted removal by a biotic agent, the forest may lose a species, but the forest structural complexity may be enhanced owing to a growth release arising from competition among the remaining species, some of which are functionally similar, leading to enhanced C uptake (**Figure 3a**, scenario 2). This scenario is likely when target species are at low density within the forest or in highly diverse systems. Third, the forest may lose a species or cohort of trees and lack structural diversity, but the remaining species may be functionally equivalent, causing the ecosystem to recover to a lower rate of C uptake (**Figure 3a**, scenario 3). This scenario may occur when a pest targets a particular species or age class or when the affected stand is recovering from a previous outbreak (as in scenario 2) and is again affected, exhibiting reduced structural diversity. Finally, the forest may not exhibit functional or structural characteristics similar to those of the predisturbance community, and C uptake rates may be diminished (**Figure 3a**, scenario 4). This scenario is likely in stands with a dominant species or monocultures where the system has to be colonized by long-distance dispersal species.

Most models utilize the theoretical approach described in scenario 1 (**Figure 3b**), in which disturbances are thought to reset successional dynamics in such a way that NPP approximates a conserved value over time (96), allowing NEP to be modeled based on disturbance frequency, extent, and specific recovery dynamics for a given system. Most biotic disturbances likely have a different dynamic of NPP recovery than in scenario 1 (**Figure 3b**). The lack of consistency in these effects makes biotic disturbance impacts on ecosystem properties difficult to model. Because disturbances are so prevalent in forests, modern silvicultural approaches in temperate systems have adopted a natural disturbance paradigm for management, attempting to mimic local disturbances and maximize ecological integrity (129). Because pests and pathogens are host specific and cause diffuse mortality at the species or genus level, recovery trajectories may follow patterns different from those in scenario 1, which are typical of fire and other abiotic disturbances (**Figure 3a,b**). Understanding how natural disturbances affect forest C dynamics and how these forces may change in the future because of climate change is critically important for the sustainability of ecosystem services provided by forests.

Forest structural complexity:

a mechanism through which forests can maintain high rates of productivity; forests comprising trees of different ages covering many different canopy strata can maximize their structural complexity

Climate forcing

factors: agents that drive the climate system to change, with some (CO₂, moisture, O₃, N₂O) directly interacting with life, causing ecosystems to change

Biological forcing

factors: biotic agents that alter terrestrial ecosystem properties, such as net primary productivity, species composition, or biogeochemical cycling; biological forcing has the potential to change the ecosystem response to climate factors at various timescales

Climate Versus Biological Forcing Factors of Forest Productivity

Climate and biological forcing factors alter plant productivity in a variety of ways. Climate—temperature, precipitation, and their combined effects via changes in vapor pressure deficit (VPD)—is a strong driver of plant and canopy C-flux rates and therefore is a primary driver of NPP and NEP (see above). Experimental manipulations (72; for other examples, see 50), simulations (32), and satellite observations (e.g., 153) have quantified negative correlations between VPD and NPP in a majority of forested ecosystems at multiple spatial and temporal scales. Climate forcing factors, such as elevated CO₂, interact with ecosystems by altering the photosynthetic and respiratory flux balance (8, 11, 30, 50, 51, 64), influencing NPP and NEP values over time. At large temporal and spatial scales, changes in NPP concurrent with global change can be large but inconsistent, with both positive and negative effects reported for different regions, ecosystem types, or timescales (e.g., 83, 94, 101, 153). As a consequence, experimental, monitoring, and modeling efforts have been devoted to untangling interactions among climate change drivers governing NPP, NEP, and ecosystem flux variability (for a review, see 86).

Ecosystem productivity monitoring efforts are highlighting the need to consider biotic and abiotic interactions in determining ecosystem properties (1, 54, 64), particularly considering the extent of the forests impacted by biotic agents (**Figure 2, Table 1**). For instance, plant physiological acclimation and adaptation to elevated CO₂ (e.g., 49), temperature (e.g., 8), and/or changes in precipitation and VPD (e.g., 17) are not widely incorporated in predictive models of the C cycle. In addition, intrinsic biotic ecosystem properties such as standing biomass, stand age, and height could govern NPP to a larger extent than temporal climate variability does (96). Results from free-air carbon dioxide enrichment (FACE) experiments suggest that factors such as species composition and resource availability explain the disagreement between observed and modeled NPP responses to elevated CO₂ (102). The relationship between abiotic factors and ecosystem responses and their associated feedbacks to climate forcing factors are further complicated by ecosystem disturbances caused by biological agents (37, 41, 62, 71, 78), such as biological invasions, which affect ecosystem properties and resilience to a different extent than abiotic disturbances (e.g., 41, 85).

Pests, pathogens, and other biotic forcing factors annually impact >20.4 million forested hectares in the United States alone, at considerable economic cost (>\$2 billion annually) (25). In fact, >15% of all US forests were affected by biological agents between 2004 and 2013 (131) (**Figure 2, Table 1**). This problem is growing and has been exacerbated by the transmission of nonnative species between continents (through global commerce) and by climate change (25, 88, 126). The relationships between forest C dynamics and abiotic disturbances (e.g., climate, fire, and drought), disturbance severity, successional dynamics, and C storage (12, 13, 15, 136) are not necessarily transferable to diffuse mortality disturbance episodes (see **Figure 3**), with perhaps the exception of drought-induced diffuse mortality. Despite the growing recognition of biotic forest disturbances (e.g., insect outbreaks and pathogens), impacts on ecosystem structure and function, their effects on the C cycle, and the associated cascading effects on ecosystems have not been comprehensively synthesized.

The variability in resilience of C uptake depends on the severity of the disturbance (proportion of stand impacted) and the time since the forest was impacted; perturbations to the C cycle associated with biotic disturbances may appear to be dampened over intermediate to long periods relative to shorter periods as surviving understory and canopy trees enter the stem exclusion phase of succession (41, 132) (**Figure 3a**). Pest and disease outbreaks that affect a specific host species or groups of species have been recently documented to affect NPP and ecosystem fluxes at magnitudes larger than those caused by climate variability (78, 98). These biotic disturbances may change successional trajectories because affected species are not present or are excluded during the recovery phase, particularly when the disturbance was caused by exotic pests.

In recent decades, the number of exotic species introduced to new habitats has increased tremendously (88). In some cases, introduced species alter the species dynamics, productivity, and biogeochemical cycling of entire ecosystems (37). The invasion of sawgrass communities by the Australian paperbark (*Melaleuca quinquenervia*) in Florida has transformed riparian grasslands into forests by causing an increase in fire frequency and size (128). Invasion of riparian zones by willow in South Africa has had a major impact on surface hydrology at the landscape scale (see 37 and references therein), inducing drought at the watershed level and reducing groundwater reservoirs. Ecosystem function and resilience are therefore susceptible to alteration by introduced pests and pathogens that target specific species. The Asian chestnut blight fungus has altered soil nutrient cycling and availability by removing dominant tree species (39). The introduction of the emerald ash borer (*Agilus planipennis*) is causing a substantial reduction of NPP in temperate forests of the eastern United States (41). These biotic interactions represent a novel set of terrestrial biological forcing factors that can induce ecosystem change comparable in scale and magnitude to impacts expected from climate change forcing factors (139, 142). In the next section, we describe specific

impacts of biotic forest disturbances (specifically pathogens and insect outbreaks) on C cycling in temperate forests.

BIOTIC FORCING FACTORS AND THEIR IMPACTS ON FOREST ECOSYSTEM DYNAMICS

The magnitude, duration, and seasonal timing of biotic disturbances disrupt forest production, altering the resilience of forests and affecting ecological interactions (1, 43); however, generalized forest responses to these disturbances remain elusive. Variability in forest responses to disturbance is likely a function of forest type (coniferous or deciduous) and disturbance type (forest pest or pathogen). Periodic defoliations that infrequently result in tree mortality, such as those caused by European gypsy moth (*Lymantria dispar* L.), result in minor perturbations to the C cycle that persist for a short time (20). In contrast, disturbances affecting larger areas and resulting in tree mortality—such as those caused by the mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins)—can have substantial, persistent effects on forest C cycling and ecosystem C storage (41, 78). The effects of biotic disturbances may be region specific and dictated by other biotic and abiotic factors as well (52). For instance, temperate forests of the eastern United States are more structurally complex, species diverse, and functionally redundant and less water limited (during the growing season) than those in the west, perhaps resulting in disturbances that perturb the C cycle less severely.

Forests and the plants therein have evolved under the constant threat of predation from insects and pathogens. Most forest insects are benign and do not inflict significant damage to trees, but under certain conditions—such as those induced by weather (14, 149), susceptible forest conditions, or damage—insect outbreaks can overwhelm plant defenses, causing mortality. Nonnative forest pests and pathogens, on the other hand, are being introduced at an alarming rate (3) and represent novel invaders in forest systems. Because forests are not adapted to nonnative pests, the pests may establish and spread without competition from natural predators (i.e., the enemy release hypothesis; see 73), causing shifts in ecosystem dynamics, as described above. One of the most notable historical examples of a nonnative pathogen was the chestnut blight, which largely eradicated the American chestnut (*Castanea dentata* Marsh.), a species that was once a major component of hardwood forests of the eastern United States (2). Unfortunately, data regarding shifts in forest productivity were not recorded for this disturbance. Below, we describe a group of current native and invasive forest pests and their impacts on forest C dynamics; these examples have been selected to highlight disturbance types (e.g., defoliation, bark borers, wood borers, and pathogens) across a wide geographic area.

Mountain Pine Beetle (Native)

Native to western North America, MPB (a bark-boring beetle) and its microbial associates are responsible for the widespread mortality of pine from Canada to Mexico. Through its species-specific impacts, MPB greatly reduces stem density and basal area for long periods following disturbances that alter species composition and structure (29). MPB activity varies among forests depending on the species composition, with a higher magnitude and increased extent of spatial synchrony in lodgepole pine (*Pinus contorta*) relative to ponderosa pine (*Pinus ponderosa*) stands (16). Spatial synchrony of MPB activity was detected in areas of low precipitation and high temperature (favorable conditions for MPB), and clustering of time-series patterns indicated that drought may act as a regional driver (16). Furthermore, analyses revealed that after MPB reached epidemic levels, its activity was more related to the lack of cold temperatures (which cause MPB mortality)

Bark-boring beetles:

beetle species whose larval or adult forms feed in or on the cambium

Defoliators: insects whose larval or adult forms consume leaf or needle material

Gross primary production: the total amount of CO₂ fixed by vegetation via the photosynthetic reduction of CO₂ into organic compounds

than to drought (16). These conditions have permitted MPB to reach levels that are greater in area and severity relative to previous outbreaks and have led to the release of significant quantities of C over large areas of British Columbia, shifting the region to a net C source (78).

Spruce Budworm (Native)

The western (*Choristoneura occidentalis* Freeman) and eastern (*C. fumiferana* Clemens) spruce budworms are among the leading causes of damage to spruce and fir forests in North America (141). Diseases, predators, and parasites contribute to population maintenance during cool, wet years, but during warm, dry years, budworm populations can reach outbreak levels. Larvae of the spruce budworm typically mine developing bud and new-growth tissue but will consume older tissue if no new tissue is available (92). Depending on their duration and severity, these defoliations can result in growth losses in excess of 50–90% and reduced cone formation (reproductive success), and because the species passes through six larval stages, continued attacks can result in mortality (see 105, 134, and references therein). Western spruce budworm outbreaks have also been suggested to result in damage to Douglas fir cones, impacting reproduction (28). Research suggests that fir mortality from western spruce budworm is highly correlated with tree volume and host density, indicating opportunities for management (90).

Forest Tent Caterpillar (Native)

Forest tent caterpillars (*Malacosoma disstria* Hübner) are defoliators of broad-leaved trees and are found throughout hardwood forests of North America; as such, they are an important forest pest. Populations fluctuate cyclically, and outbreaks occur at ~5–15-year intervals, triggered by mild winters (146). Because these caterpillars are active early in the growing season, they reduce tree growth, occasionally leading to mortality (57, 150). A study of 47 forests in New York and Vermont that had been defoliated by forest tent caterpillars identified drought as the second-most-important factor causing sugar maple mortality (150). The interactions between biotic forcing factors and climate may be mediated by changes in soil moisture and canopy openness (150). Light-use and production efficiency models to predict photosynthesis and net C exchange during forest tent caterpillar defoliation revealed an ~79% reduction in NEP, primarily driven by reduced gross primary production, increased ecosystem respiration, and increased leaf and frass decomposition during the year of impact (22).

Emerald Ash Borer (Nonnative)

Emerald ash borers (*Agrilus planipennis*) are nonnative, invasive, phloem-boring beetles that were accidentally introduced into the United States in the late 1990s (130). With the assistance of human-mediated transport in the form of transported nursery stock, firewood, and hitchhiking, they have been rapidly spreading across the Great Lakes region, leaving millions of dead ash trees in their wake (114). The larvae feed in the cambium of native ash trees (*Fraxinus* spp.) > 3 cm in diameter, creating serpentine galleries that affect water and nutrient dynamics and lead to mortality in as little as two to five years (41, 42, 117). Targeting of canopy and subcanopy ash by these beetles has resulted in declines in aboveground NPP, shifts in species compositions, and an orphaned cohort of ash seedlings, which, depending on continued pressure from these beetles, may ultimately be eradicated from forests (41, 76). The recent discovery of emerald ash borer larvae and exit holes on white fringetree (*Chionanthus virginicus* L.) highlights the unpredictable consequences of invasive forest pests and indicates that our understanding of the pest-host interactions remains unclear (19).

Gypsy Moth (Nonnative)

Accidentally introduced into North America around 1868, the European gypsy moth (*Lymantria dispar* L.) is a defoliator with a broad host range that includes more than 300 deciduous and coniferous species (5, 38). Gypsy moth outbreaks usually last two or three years before collapsing and remain low for approximately ten years. In the Pine Barrens of New Jersey in the United States, gypsy moths reduce peak net ecosystem exchange (NEE) (June–July) by 60% during the first year of the outbreak and by 90% during the second year (20). These outbreaks leave impacted trees more susceptible to other pest and pathogen agents. Spread rates of gypsy moth are related to winter temperatures, indicating a potential climatic constraint on the species (79). Therefore, milder winters can provide a positive feedback on the spread of gypsy moth.

Beech Bark Disease (Nonnative)

Beech bark disease primarily affects beech trees (*Fagus grandifolia* Ehrh.) and is a complex consisting of an exotic scale that alters beech bark and leaves it to be colonized by *Neonectria* sp. and subsequently decaying fungi (65). Established in North America in the late 1800s in Nova Scotia, it has been slowly moving across the forests of the northeastern United States and Canada. The disease has been causing a decline in beech stems, a shift in litter from beech to sugar maple (*Acer saccharum* Marshall), and a decline in the basal area of beech trees (58). Forest plots exhibiting elevated levels of beech bark disease also exhibited reduced fluxes of soil-respired CO₂, suggesting reduced photosynthetic uptake or gross primary production (58). Over time, with continued beech bark disease pressure, these historically beech-maple forests may shift in dominance toward sugar maple.

Dutch Elm Disease (Nonnative)

Dutch elm disease, which affects all native elm species (*Ulmus* spp.) in North America, is caused by the nonnative fungus *Ophiostoma novo-ulmi*, which was introduced into North America in the early 1930s. The disease is transmitted between mature trees by two insect vectors, the native elm bark beetle (*Hylurgopinus rufipes*) and the European elm bark beetle (*Scolytus multistriatus*). Infection leads to high mortality, eliminating large trees of ecological importance from a large geographic area (see 84 and references therein).

ASSESSING THE IMPACTS OF FOREST PESTS ON FOREST CARBON DYNAMICS

To evaluate the relationship between forest C cycling parameters and biotic disturbance types, disturbance severity, and times since disturbance, we conducted a review of field and modeling studies. Using Web of Science, we conducted two searches to identify relevant literature: (a) one for “forest and pest and producti*” on or before January 20, 2014, and (b) one for “forest and carbon and disturbance and eddy covariance” on or before January 21, 2014. These searches yielded a total of more than 500 papers, of which only 12 contained data structured appropriately, i.e., with a control and data regarding C cycling, NPP, NEP, NEE, or net biome production, precluding the use of a formal meta-analysis. We recognize that controls are difficult to have while investigating biotic disturbance effects because the disturbing agent may be widespread and comparisons are often restricted to before and after the event. Data used in our analyses were acquired either from the authors or from DataThief III. In collecting these data, we hoped to address two primary questions. First, do pests and pathogens have differential impacts or legacies on forest C cycling? And second, to what degree does disturbance severity impact forest C cycling?

Net ecosystem exchange (NEE): a measure of the amount of the net fixation of atmospheric C entering the ecosystem per unit of time

Net biome production: equivalent to net ecosystem production at regional or global scales, and typically used to include C losses during disturbances

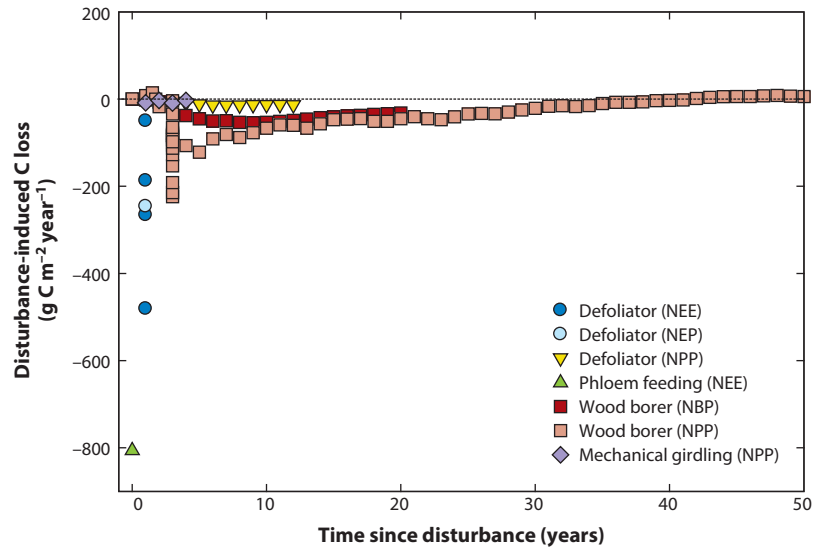


Figure 4

Effects of biotic forcing factors on forest C uptake following disturbance. Data are derived from References 20, 22, 31, 35, 41, 52, 78, 97, and 138. The different symbols denote different C-flux approaches. Abbreviations: NBP, net biome production; NEE, net ecosystem exchange; NEP, net ecosystem production; NPP, net primary production.

Do Pests and Pathogens Have Differential Impacts or Legacies on Forest Carbon Cycling?

Despite the paucity of data (particularly the lack of studies that examine similar species across a broad set of conditions and use comparable C accounting metrics), our findings support the consensus that biotic forcing factors differentially affect forest C uptake depending on the agent and stand characteristics (**Figure 4**). Data indicate that defoliators cause substantial short-term impacts on forest C uptake (20, 22, 31) (**Figure 4**). These moderate to severe short-term reductions in C uptake are associated with herbivore-induced photosynthetic reductions, which typically do not persist for long periods (but see 89). The severity of defoliation's effect on the C cycle depends on the physiology of the affected species. For instance, indeterminate species can reflush leaf tissue following defoliation, thereby minimizing C loss, whereas determinate species must forgo photosynthetic returns until the following growing season (77). Bark- and wood-boring beetles, on the other hand, gradually affect targeted trees, manifesting in mortality across several years (35, 41) (**Figure 4**). This gradual mortality allows understory species to fill in canopy gaps as they form, thereby buffering ecosystem C losses (**Figure 2**). However, as trees impacted by bark and wood borers succumb, they reduce ecosystem C uptake and contribute to the coarse woody debris pool, which can contribute substantially to C losses over time as downed trees decompose (53).

Wood-boring

beetles: beetle species whose larval or adult forms consume wood

To What Degree Does Disturbance Severity Impact Forest Carbon Cycling?

Successional theory suggests that increasing disturbance severity leads to increasing impacts on forest C dynamics (see A Historical Perspective on Forest Succession and Disturbance, above). Yet the literature denoting disturbance severity and changes in aboveground net primary production (ΔNPP_W) is limited because disturbance severity is difficult to quantify at increasing scales (from

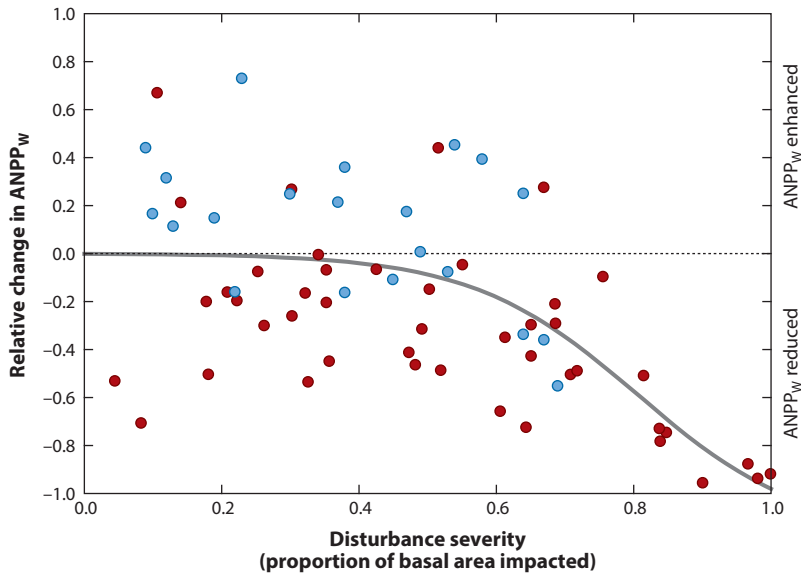


Figure 5

Relationship between disturbance severity and the relative change in aboveground net primary production ($ANPP_W$) associated with emerald ash borer–induced ash decline in temperate forests in northwestern Ohio (red circles) and mechanical girdling in a mixed deciduous forest in northern Michigan (blue circles) (for data, see 41 and 132, respectively). The dashed line at $y = 0$ separates disturbance-enhanced $ANPP_W$ from disturbance-reduced $ANPP_W$; the solid gray line denotes the best-fit sigmoidal three-parameter model relationship for the composite data set ($R^2 = 0.3923$, $P < 0.0001$).

plot to landscape). Data extracted from the literature indicate that as the disturbance severity or the proportion of the basal area impacted increases, the relative change in $ANPP_W$ decreases (Figure 5). Furthermore, the relationship is sigmoidal rather than linear: The reduction in the relative change in $ANPP_W$ becomes greater as the disturbance severity increases.

These biological agents can impact forest productivity and ecosystem C fluxes at magnitudes similar to those of climate forcing factors (34, 41, 54, 78). Additionally, because comparable areas of forest may be affected by pests and pathogens relative to abiotic disturbances (Figure 2), observations and monitoring efforts to discern effects of climate forcing factors and climate variability on forest productivity should take biological factors into account.

INTERACTIONS BETWEEN CLIMATE CHANGE AND FOREST PESTS AND PATHOGENS

An intriguing component of biotic disturbance is the interaction between climate change and the susceptibility of forests to present or future disease outbreaks. Mean annual global temperatures are expected to increase by 1.8–4.0°C over present temperatures during the twenty-first century (66). In addition to increases in mean temperature, climate change models predict more heat waves and fewer cold waves (33). Regions of North America may experience even greater temperature shifts, particularly during the winter at higher latitudes and during the summer in the middle of the continent (26) and the eastern United States (87). Increased temperatures will occur concurrently with shifts in the timing and magnitude of precipitation events (93) and other severe stochastic weather events, which can create uncertainty in predicting forest responses to climate change.

These climate factors are responsible for extending growing season length, northward migration of tree species, or altered phenology (107), which may alter C uptake and allocation to labile carbohydrates and enhance NPP. However, climate change is also responsible for the increase in the frequency and severity of forest disturbance, including insect and disease outbreaks (25), which may decrease regional and global forest productivity. For instance, drought stress is almost ubiquitous to all forests. Drought exposure time and severity combined with ecosystem and soil type may cause age-dependent mortality (shallow-rooted young trees may be more susceptible to drought than deep-rooted old ones), increase wildfires, or enhance the susceptibility of forests to pest outbreaks (100).

Increased temperatures and altered precipitation regimes (93) will directly alter plant and pest phenology, plant physiology, and plant distributions while indirectly affecting the ability of plants to resist forest pests and pathogens (145). Warming is likely to increase the extent and severity of native insect pests (82) and perhaps facilitate the spread and impact of introduced pests and pathogens. On long timescales, northward migration of temperate forest species can increase the range of their associated pests. Moreover, relative to the life spans of most trees, insect generation times are short, enabling insect species to better adapt to climate change and thereby giving them an advantage over their plant hosts. The interactions between temperature and insect physiology are well established and have been incorporated into forest models to help predict herbivory effects on forest productivity (143), suggesting that climate change will lead to an increase in forest susceptibility to pests and pathogens (145).

In response to pest and pathogen pressure, plants can shift their foliage quality to tissue that is lower in protein but higher in fiber, tannins (hydrolyzable and condensed), or total phenolics, all of which reduce larval survival and fecundity (122, 125). Plant defenses can therefore regulate herbivore populations (36; but see 135, which indicates that the parasitoid–larch bud moth interaction is the dominant driver of population growth rates). Despite the efforts of trees to resist some forest pests via secondary metabolism, insects such as MPB may be able to overcome these efforts via pheromone-mediated mass attacks (115). Further increases in temperature can affect the life cycle of bark beetles, boosting population size and facilitating mass attacks (10). Moreover, many host species presently live outside the optimal climate envelope (e.g., temperature and moisture) that their associated pests need in order to be effective. Climate change has already been observed to affect forests by altering the local climate, increasing the frequency of outbreaks in previously low-risk areas (99). The responses of pest predators, competitors, or mutualistic partners to climate change are less well known but are of recognized importance for forest sensitivity to biotic disturbances (43).

Because forest pests are ectotherms, their development is constrained by temperature. Thermal requirements for the survival and development of forest pest larvae are species specific and normally distributed (116). Climate change, particularly global warming and shifts in precipitation, will directly affect the population dynamics and geographic distribution of forest pests in two primary ways. First, warming will reduce mortality events caused by cold temperatures and will allow pests to invade higher-elevation areas (9, 69). Second, warming will alter temperature-mediated life-history events, leading to earlier phenological events (i.e., larval development and emergence) (4). Larval development relates to temperature in bark borers (9, 59), non-bark-boring beetles (103), leaf miners (68), and folivorous insects (127), with warmer temperatures resulting in shorter development. Warmer temperatures may also shift the life cycles of some forest pests from univoltine to semivoltine, potentially leading to synchronized emergence, mass attacks, and more severe pest outbreaks (59). Warming has also led to a decline of larch bud moth (*Zeiraphera diniana* Gn.) outbreaks across the European Alps (69). During host tree colonization, bark beetles introduce and rely on a variety of symbionts (e.g., bacteria, fungi, nematodes, and mites),

which are sensitive to host tree chemistry, moisture, and temperature. Bark beetle success may be indirectly influenced by symbiont responses to changes in temperature and precipitation (75), although studies often neglect these interactions.

Warmer climatic conditions will allow forest pests to invade regions from which they were previously excluded because of low winter temperatures, specifically higher-latitude and higher-elevation areas (7, 108, 109, 121, 148). Research has revealed range expansions of two geometrid moths, *Operophtera brumata* Bkh. and *Epirrita autumnata* L., in northern Norway (67). Specifically, the less cold-tolerant *O. brumata* moved poleward, whereas the more cold-tolerant *E. autumnata* exhibited continental expansion as the climate in the region warmed. The outbreak duration of the eastern spruce budworm in eastern Canada has been linked to the accumulation of spring growing degree days, and outbreak severity has been linked to spring maximum temperature (56).

The positive effects of climate change on larval development may be partially offset by increased rates of parasitism because longer growing seasons allow more generations and larger populations of parasitoids (104, 127). Parasitism has been suggested to be a significant regulator of forest pest population dynamics (135). More rapid development may reduce forest pests' susceptibility to larval predators and parasitoids (43, 74, 120, 140), although evidence suggests that parasitoid activity may be heightened during warmer conditions, causing increased rates of larval parasitism (140).

Larval development has also been linked to CO₂ concentrations, with increased CO₂ resulting in earlier emergence (68). In response to atmospheric CO₂, trees can accumulate more C and increase the C-to-N ratio of tissues, resulting in compensatory feeding from herbivores but slowing the herbivory growth rate. Increased levels of atmospheric CO₂ can also lead to increases in C-based plant defenses and a decrease in N-based defenses and terpenoids (119). It is unclear, however, how plant accumulation of defense compounds and decreases in N content in response to elevated CO₂ will affect future biotic disturbances, as very few studies have investigated these interactions. This reduction in tissue N is even more critical for phloem-feeding insects, as we found only one study that linked phloem chemistry in response to elevated CO₂ to infestation success (an investigation of cotton infestation by *Aphis gossypii* via compensatory feeding; 133). The interactions between CO₂ and drought in particular may prevent plants from producing adequate defenses against pests and pathogens.

Plant drought stress may cause C starvation and cavitation, leading to widespread mortality at ecosystem and regional scales. Reduced NPP caused by drought increases the susceptibility of forests to pests and pathogens owing to plants' reduced effectiveness in fighting mass attacks, particularly in dense stands, where competition for resources may be more critical. Therefore, changes in temperature, atmospheric CO₂ concentrations, and precipitation patterns expected from climate change scenarios may be detrimental to the health of tree species, making them more susceptible to existing or novel pests and pathogens.

The positive responses of forest pests to climate change may result in positive feedbacks to the climate system. Increased outbreak severity over a larger range will result in larger inputs of woody debris into forest systems, creating hazardous fuel conditions (41, 78, 98). An increased susceptibility of beetle-impacted areas to forest fire can result in increased emissions of terrestrial C into the atmosphere, further exacerbating warming. These feedbacks have been investigated in low-diversity western US forests (60, 61) but have been almost entirely neglected in diverse deciduous or mixed forests (91).

CONCLUSION

Native and introduced pests and pathogens will be as important as climate change in determining forest dynamics in the future (78). In fact, introduced pests and pathogens are an increasingly

Phloem-feeding insects: insects from the order Hemiptera that feed on phloem sap

Table 2 Suggested future research needs along with potential experimental and modeling approaches for understanding the effects of biotic forcing factors on ecosystem dynamics

Issue	Experiments	Modeling
Tree- and stand-level physiological responses to pests and pathogens	Measure gas exchange, sap flow, use of reserves, or allocation of impacted and neighboring nonimpacted species	Develop a hierarchical process-level understanding of biotic interactions
Integration of physiology and phenology and stand complexity in responses to biotic agents of disturbance	Monitor NPP and resource use of the ecosystem as a function of severity of impact at the stand level and as a function of canopy complexity and diversity	Parameterize positive and negative effects of biotic interactions on NPP and other ecosystem properties
Effects of biological forcing on biogeochemical cycling	Measure changes in NPP, C storage, NEP, ecohydrology, and nutrient dynamics as a function of diversity, or stand age and time since disturbance	Evaluate the importance of forest resilience and response to biotic and abiotic stressors
Climate and biological forcing interactions	Evaluate how impacted and nonimpacted forests respond to the changes in the abiotic environment	Untangle the biological interactions affecting most short-term observations from long-term trends in response to climate forcing factors and climate change
Invasive species and biodiversity	Perform manipulative experiments to untangle how ecosystem function is affected by the decrease in biodiversity or introduction of exotic species after a biotic disturbance	Consider multiple trajectories of ecosystem recovery from disturbance that may lead to a structurally and functionally distinct ecosystem

Abbreviations: NEP, net ecosystem production; NPP, net primary production.

important component of forest biotic disturbance in North America (145). Although transportation and trade are the major reasons for the introduction of exotic pests and pathogens, changes in climate make forests more vulnerable to these disturbance agents, at least in some cases [e.g., *Dothistroma* needle blight (*Dothistroma pini* Hulbary and *D. septosporum*), which affects a wide host of pines across North America; see 6 and 144]. Climate-driven disturbance can also pave the way to infestation success by introduced pathogens because host species will be less able to trigger defenses and a reduced number of individuals will be needed for an effective mass attack. In some cases, such as the emerald ash borer, host *Fraxinus* species are defenseless, causing rapid mass mortality of infected individuals and stands (41).

This review and the successional theory presented herein provide a useful framework for studying pest and pathogen impacts on forest dynamics and their cascading feedbacks on climate. This review also highlights the paucity of data regarding the sink strengths of forests in response to these disturbances. **Table 2** lays out the suggested future research needs, associated experiments, and implications for modeling. The availability of long-term data sets, such as those derived from Long Term Ecological Research (LTER) Network sites, provides a valuable baseline against which to quantify ecosystem responses to biotic forcing factors (137). Unfortunately, these data sets are sparse, and many were not initially deployed to detect forest dynamics associated with biotic disturbance agents. Deployment of mobile flux towers [e.g., the National Ecological Observatory Network (NEON)] in advance of impending biotic disturbances could bolster our understanding of forest C dynamics. Finally, long-term studies should be undertaken to understand the interactions among stand-level physiological responses to pests and pathogens, climate forcing factors, and invasive species, because the postdisturbance communities of diverse forest systems (such as the Catskill Mountains in New York State, United States) are also susceptible to a variety of pests and pathogens as well as climate change (85).

SUMMARY POINTS

1. Forest pests and pathogens can act as biological forcing agents of ecosystem change by causing rapid, diffuse mortality of functional groups or species; impacting forest productivity; and altering the energy and carbon exchange of forests with the atmosphere.
2. Data extracted from the published literature indicate that relative to defoliators, wood-boring beetles have the greatest impact on forest productivity, shifting forests from carbon sinks to sources.
3. Forest structural complexity may provide a resilience mechanism that buffers productivity losses associated with pest- and pathogen-induced mortality.
4. There is a nonlinear relationship between disturbance severity and changes in above-ground net primary production, whereby forests that are lightly impacted by biotic disturbances have some resilience, but as a greater proportion of a forest is impacted, it ceases to be resilient.
5. The frequency and severity of forest pest and pathogen outbreaks may become more severe in a warming climate, and the consequences of these potential impacts to the climate system at the local and global levels are unknown.

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