

The Effects of Biotic Disturbances on Carbon Budgets of North American Forests

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Abstract

Forest insects and pathogens are major disturbance agents that have affected millions of hectares in North America in recent decades. The extensive area of outbreaks and large number of trees affected suggest significant impacts to the carbon (C) cycle. Here we present a review and synthesis of published studies of biotic forest disturbances in North America and their effects on C budgets. Substantial variability exists among major disturbance agents in terms of area affected, life history and drivers, and effects on trees. Insects and pathogens can greatly affect carbon budgets. Primary productivity can be reduced considerably following insect or pathogen attack. Following repeated growth reductions or a single infestation by some bark beetles, tree mortality can occur, modifying subsequent stand-level productivity and decomposition for decades. Net C sinks may be reduced following attack, with stands often becoming C sources. Recovery of C stocks and fluxes following disturbance is influenced by the number of trees killed and presence of remaining vegetation, including herbs, shrubs, and trees. We identified substantial knowledge gaps regarding the extent, drivers, and dynamics of biotic disturbance agents and their C cycling impacts, including comparisons across disturbance types and times since infestation and behavior at landscape and regional scales. We conclude that although these outbreaks are broad-scale and highly significant forest disturbances, the limited knowledge about biotic agents, few number of C cycle studies, and diversity of outbreak conditions impart large uncertainties for quantifying effects on North America's carbon budget.

1. Introduction

Atmospheric CO₂ is a key driver of past and predicted future climate change [IPCC, 2007]. In addition to anthropogenic emissions of carbon (C) from fossil fuel burning and other activities, exchange of C with the biosphere is crucial for governing the amount of CO₂ (the primary anthropogenic greenhouse gas) in the atmosphere [CCSP, 2007]. Biogenic fluxes of C occur mainly through the interplay of CO₂ uptake by plants (photosynthesis) and release of C back into the atmosphere via autotrophic and heterotrophic respiration (the latter also known as decomposition).

There is considerable interest in quantifying the North American carbon budget that has, in part, been driven by national and international reporting obligations [Chapin *et al.*, 2008; Kurz *et al.*, 2008b]. Over the past few decades, North American terrestrial ecosystems are thought to have been a carbon sink as a result of forest regrowth following harvest in past centuries, woody encroachment, and sequestration by wetlands and agricultural soils [CCSP, 2007]. The First State of the Carbon Cycle report estimated a North America sink of 0.5 Pg C yr⁻¹ (1 Pg C = 10¹⁵ g C = 1 Gt C = 1 billion metric tons of C) in 2003, though with large uncertainty [CCSP, 2007]. Reducing this uncertainty to increase confidence in future predictions of C dynamics and support climate change adaptation and mitigation activities will require research to quantify the magnitude of C sources and sinks and their spatial patterns and controls [Denning, 2005].

Forests play major roles in the global carbon budget through their influence on the dynamics of the terrestrial carbon cycle [Bonan, 2008; Canadell and Raupach, 2008]. Forests contain 422 Pg C, 76% of the C in terrestrial vegetation and about the same amount as in the atmosphere [Houghton and Skole, 1990]. In the Northern Hemisphere, forests are major carbon

sinks, taking up 0.6-0.7 Pg C yr⁻¹ [Goodale *et al.*, 2002], about 12% of the annual emission of CO₂ by humans [Schimel *et al.*, 2001]. Human and natural changes to forests and environmental conditions have resulted in significant effects on the global carbon cycle. For example, large releases of carbon to the atmosphere have been reported from tropical deforestation [Canadell *et al.*, 2007] and fire and insect outbreaks [Kurz *et al.*, 2008b].

Insects and pathogens are agents of significant disturbance in North American forests. Many outbreaks are highly localized, but some range across millions of hectares and may affect up to 45 times the area of wildfire [Dale *et al.*, 2001]. These disturbances in the US have an average annual economic cost of \$1,500,000,000, five times that of wildfire [Dale *et al.*, 2001]. Wood volume lost to insects in Canada from 1977-1987 was nearly 1/3 of harvest volume, on par with volume lost to disease, and exceeds that from fire [Fleming, 2000]. Insects can have substantial effects on forest productivity [Maclean, 1990b], causing, for example, growth loss and mortality that exceeds 50x10⁶ m³/year in Canadian forests [Fleming, 2000]. The large areas of tree mortality or reduced tree growth resulting from major epidemics suggest substantial impacts to the North American carbon cycle. Additionally, biosphere-atmosphere exchanges of carbon influence climate, and climate is an important driver of insect and disease outbreaks [Ayres and Lombardero, 2000; CCSP, 2008]. Thus, important feedbacks exist between climate change and biotic disturbances through the carbon cycle.

Here we review the effects of forest insect and disease disturbances on the North American carbon cycle. We focus on major biotic disturbance events, which we define as large (>100 km²) forest areas affected by insects or disease over time scales less than a decade. We do not consider smaller disturbance events or background herbivory or disease, which we recognize

as important, but instead concentrate on those outbreaks with significant impacts to the North American carbon cycle.

Our review is written for carbon cycle scientists interested in learning more about biotic disturbances and for scientists and land managers familiar with insects and pathogens who want to learn more about how these agents affect carbon budgets in forests. We describe the major insect and pathogen disturbance agents in North American forests and provide an overview of the extent of biotic disturbances in the region. We discuss drivers of outbreaks and note interactions with other disturbance agents. We then review the impacts to the carbon cycle, including expected responses as well as studies that document the influence of insects and pathogens on carbon cycling. We end by identifying gaps in knowledge and describing tools available for closing these gaps.

2. Major insect and pathogen species contributing to forest disturbance

2.1 Insects

Insects contribute highly to the species diversity of terrestrial ecosystems. Most insects exert relatively chronic background herbivory and do not undergo large-scale outbreaks. However, a few have acute landscape-scale impacts, existing at barely detectable levels for extended periods and then rapidly irrupting to outbreak levels with substantial impacts on forests. It is these landscape-level insect outbreaks that likely have the largest implications for forest carbon cycling. The major tree-level impacts caused by insects include growth reduction, predisposition to subsequent biotic and abiotic stress agents, vectoring or creating infection

courts for phytopathogens, and tree mortality. Each of these tree-level impacts may amplify to stand- and landscape-scale impacts such as canopy thinning, gap formation, or alterations in species composition, stand architecture, and successional trajectories [Raffa *et al.*, 2008].

Here we discuss the major insects of deciduous and coniferous forests common to the United States and Canada (Table 1). All of these insects may cause significant growth reductions, tree mortality, or both [Maclean, 1990a]. Areas affected by several representative species were compiled to illustrate variability among species and variability over a 9-year time series from 1999-2007 [Natural Resources Canada, 2009; USDA Forest Service, 2000; 2002; 2003a; b; 2004; 2005a; 2006; 2007; 2009c]. These time series illustrate that outbreaks of some insect species are more extensive than others, the timing of outbreaks varies among species and across regions, and major outbreaks occur throughout North America (Figure 1).

2.1.1 Bark beetles

Bark beetles (Coleoptera: Curculionidae: Scolytinae) feed within phloem and exert the highest forest impacts of any insect group. Most important species are native. This large group of insects can be classified according to the physiological condition of trees they typically colonize. Most species colonize dead trees, and most of the remainder colonize stressed trees. A few bark beetle species kill healthy trees, generate their own positive feedback with respect to population dynamics, and exert landscape-scale impacts. Tree-killing bark beetles exhibit highly eruptive dynamics, and typically reside in an endemic condition, during which a suite of biotic and abiotic constraints limits their reproductive success. Large-scale factors such as canopy structure, forest homogeneity, and regional climate affect microscale interactions that determine

whether various thresholds are breached that lead to epidemics, and conversely, outcomes of microscale interactions have landscape-scale consequences [Raffa *et al.*, 2008]. All of the tree-killing bark beetles have close associations with fungi, and most are host-specific at the level of tree genus.

Notable bark beetle species include mountain pine beetle (*Dendroctonus ponderosae* Hopkins), which attacks pines across western North America (Table 1). Major outbreaks have occurred in the past, with extensive epidemics ongoing in British Columbia and Colorado, among other locations, and large losses expected in the near future [Krist *et al.*, 2007; Kurz *et al.*, 2008a]. Another major insect, spruce beetle (*Dendroctonus rufipennis* Kirby), is considered the most important insect of spruce-fir forests in western North America and is one of the major biotic disturbance agents in Alaska [USDA Forest Service, 2009c]. Southern pine beetle (*Dendroctonus frontalis* Zimmermann) occurs across the southeastern US, attacking multiple species of pines over large areas, and is predicted to cause large losses (54 Mm²) of basal area in the next 15 years [Krist *et al.*, 2007]. Various *Ips* species in combination with severe drought were responsible for a major mortality event in pinyon pine (*Pinus edulis* Engelm.) in southwestern US in the early 2000s. Western balsam bark beetle (*Dryocoetes confuses* Swaine) is currently killing subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) across the western US.

2.1.2 Defoliators

Defoliators also exert a high level of impact on tree growth and mortality, but their effects are substantially different from those of bark beetles. Defoliators are the largest group of insects affecting trees and include several orders, of which Lepidoptera is most important. The

most common effects of folivory are reduced growth and reallocation of carbon, although repeated severe defoliation may cause tree mortality [Candau *et al.*, 1998; Elkinton and Liebhold, 1990]. Some defoliator species undergo dramatic cyclic or intermittent population outbreaks [e.g., *Zeiraphera diniana* Gn., larch budmoth, Esper *et al.*, 2007], but most exert more chronic effects. Folivores do not have the “all or nothing” relationship with their hosts that is characteristic of bark beetles (i.e., killed tree versus failed attack), and tree defenses more often affect insect size, development time, and fecundity [Stevens *et al.*, 2007].

Most leaf-feeders are host-specific at the level of tree genus, but in North America two major species, forest tent caterpillar (*Malacosoma disstria* Hubner) and gypsy moth (*Lymantria dispar* L.; discussed below), have very broad feeding ranges (Table 1). Forest tent caterpillar is a major defoliator of several deciduous trees and has a wide distribution in North America, but has had relatively few reports of widespread mortality [Volney and Fleming, 2000]. Severe defoliation in combination with climate-related drought, however, is resulting in increasing areas of aspen (*Populus tremuloides* Michx.) decline [Allen *et al.*, 2010; Hogg *et al.*, 2008].

Budworms feed primarily on the buds of new conifer needles, and defoliation over several years can lead to tree mortality by constraining tree growth or vigor and preventing establishment of needles. Eastern spruce budworm (*Choristoneura fumiferana* [Clem.]) causes more damage than any other insect in North America’s boreal forests [Volney and Fleming, 2000]. Western spruce budworm (*Choristoneura occidentalis* Freeman) is considered the most widely distributed and destructive conifer defoliator in western North America [Fellin and Dewey, 1982].

2.1.3 Major invasive insect species

Species compositions and relationships are shifting rapidly with accelerated introductions accompanying intercontinental trade [Liebhold and Tobin, 2008]. The underlying causes behind the severe impacts of invasive insects can be classified into two main categories, although each instance is a blend of many forces. First, some insects such as gypsy moth are more eruptive in their introduced region because this region lacks the natural enemy complex present in the native range. Second, a lack of coadaptation between the introduced insect and its new host leads to low resistance and or tolerance [Gandhi and Herms, 2009]. For example, emerald ash borer (*Agrilus planipennis* Fairmaire) colonizes only highly stressed or dead trees in its native Asian range, as opposed to commonly killing live trees of the genus *Fraxinus* where introduced in North America [Kovacs *et al.*, 2010; Poland and McCullough, 2006]. Likewise, hemlock woolly adelgid (*Adelges tsugae* Annand) is better tolerated by coadapted trees within its native range, allowing predators time to respond and potentially reduce populations; this lack of coadaptation of trees in the adelgid's introduced range does not permit a similar predator response. Although both mechanisms occur, the latter source of outbreak dynamics (lack of host adaptation) is more threatening to tree species. Some invasive insects are more cryptic than others and so their effects are often unnoticed. For example, a complex of root-feeding weevils is currently affecting fine root processes in northern hardwood ecosystems (Table 1).

Two invasive insects are important forest disturbances whose carbon cycle consequences have been studied. Gypsy moth is an invasive species in North America that was established in the middle of the 19th century and spread throughout the eastern US [USDA Forest Service, 2009c] and eastern Canada [Régnière *et al.*, 2009]. This exotic insect is projected to affect 41

Mm² of basal area within the next 15 years [Krist *et al.*, 2007]. A major disturbance agent in forests of the eastern US, the hemlock woolly adelgid attacks hemlocks (*Tsuga* spp.), feeding on tree fluids. Hemlocks in this region have poor natural defenses against or tolerance of hemlock woolly adelgid, leading to high mortality probability from outbreaks.

2.2 Pathogens and declines

A plant disease is defined as “any malfunctioning of host cells and tissues that results from continuous irritation by a pathogenic agent or environmental factor and causes symptoms” [Agrios, 2005]. Here we focus on pathogens, including infectious diseases (Table 2). Forest pathogens are taxonomically diverse and include fungi, bacteria, viruses, nematodes, and parasitic plants. Fungal pathogens, which are the most common causes of forest diseases, are primarily in the phyla Basidiomycota and Ascomycota [Durall *et al.*, 2005]. Many forest pathogens are specific to a host genus (e.g., *Cronartium ribicola* J.C. Fisch on *Pinus* spp.), others have a wide host range including both coniferous and deciduous species (e.g., *Armillaria* spp.), and a few are host-species specific (e.g., most dwarf mistletoes).

Native forest pathogens tend to act more slowly than other disturbance agents but their effects on carbon cycling can be dramatic, causing significant damage to trees by killing them, slowing their growth, predisposing them to windfall or insect attack, and/or affecting overall wood quality [Hansen, 2000; Tkacz and Hansen, 1982; Woods *et al.*, 2005]. Although some pathogens kill trees that are already stressed or weakened, others (e.g., root pathogens) are able to kill vigorous, dominant trees [Hansen and Goheen, 2000]. Estimates of plant pathogen impacts in North America are not well documented, but some figures are available. Harausz and

Pimentel [2002] reported that pathogens have affected approximately 17.4 million ha and 6% of total annual production in the US. Average Canadian losses in 1982-1986 have been estimated at 45 million m³ per year, which is approximately 16% of production [*Singh*, 1993].

We briefly describe some of the most important functional groups of pathogens (Table 2). Cankers occur as localized wounds or dead areas in the bark of stems or branches. Native cankers generally deform and reduce the growth of trees and predispose them to more destructive agents, although some occasionally girdle trees completely [*Agrios*, 2005]. Important invasive canker fungi include chestnut blight (*Cryphonectria parasitica* (Murrill) Barr.), which has extirpated American chestnut (*Castanea dentate* (Marshall) Borkhausen) through the eastern US [*Loo*, 2009], and beech bark disease (*Neonectria* spp.).

Foliar pathogens defoliate trees to varying degrees, reducing photosynthetic capacity and causing concomitant growth loss. Foliar fungi are very sensitive to changes in environmental conditions and can be particularly damaging to host trees planted outside their current range [*Kliejunas et al.*, 2009]. Major outbreaks of *Dothistroma* needle blight and Swiss needle cast (*Phaeocryptopus gäumannii* (Rohde) Petrak) have occurred in western North America.

The hyphae of vascular wilt and some blue-stain or sapstain fungi kill trees by plugging their hosts' water- and nutrient-conducting tissues. These fungi are often vectored by insects, such as in the case of Dutch elm disease, a pathosystem that includes species of *Ophiostoma* and two species of bark beetles. Bark beetle-vectored fungi such as *Grosmannia clavigera* (Robinson-Jeffrey and Davidson) Zipfel, de Beer and Wingfield may assist beetles in overcoming tree defenses [*Lieutier et al.*, 2009] and may also be moderately pathogenic [*Plattner et al.*, 2008], although their specific roles remain in dispute [*Six*, 2003].

Root disease fungi usually infect trees through the root system. Many pathogenic root fungi readily infect and kill healthy, otherwise unstressed trees and have long-term impacts on tree growth and survival and on overall forest productivity [Cruickshank, 2000; Cruickshank *et al.*, 2009; Klepzig *et al.*, 1991]. Armillaria and Annosus root diseases have the most widespread occurrence in the forests of North America [Goheen and Otrosina, 1998]. In Canada, stem and root rots have destroyed 25 million and 24 million m³, respectively, of timber per year [Singh, 1993].

Rust fungi require live hosts and usually two botanically unrelated hosts to complete their life cycle. The most important rusts in North American forests are the stem and cone rusts of pines [Sinclair *et al.*, 2005]. The native fusiform rust (*Cronartium fusiforme* Hedgcock & Hunt ex Cummins) infects loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* var. *elliottii* Englem.) in the US [Phelps and Czabator, 1978]. The invasive white pine blister rust fungus (*Cronartium ribicola* J.C. Fisch Ex. Raben) has severely diminished five-needle pine populations across much of their range in Canada and the US [Geils *et al.*, 2010; Kinloch, 2003; Maloy, 1997].

Phytophthora species infect a wide variety of hosts and have been responsible for severe forest epidemics worldwide, such as the recent sudden oak death epidemic in California and Oregon caused by *Phytophthora ramorum* sp. nov. The success of *Phytophthoras* as pathogens is due in part to their rapid reproduction under favorable environmental conditions, which allows inoculum levels to increase to high levels within a few days or weeks [Kliejunas *et al.*, 2009].

Dwarf mistletoes (*Arceuthobium* spp.) are parasitic vascular plants causing significant impacts to a range of conifer species in North America [Geils *et al.*, 2002; Hawksworth and

248 *Wiens, 1970; Loomis et al., 1985; Singh, 1993*]. Dwarf mistletoes reduce host growth and
249 increase tree mortality and susceptibility to other damage agents.

250 The term “forest decline” describes stands and/or landscapes where trees, typically of a
251 single species, progressively lose vigor and often die, frequently due to a complex of abiotic and
252 biotic factors [*Klepzig et al., 1991; Manion and Lachance, 1992*]. Although declines are not
253 solely caused by biotic agents, insects and pathogens may amplify the effects of the predisposing
254 stress factors [*Raffa et al., 2008*]. A current example of decline is sudden aspen decline in
255 western North America, the causes of which have not yet been delineated [*Worrall et al., 2008*].
256 Decline events can result in widespread, cumulative mortality with a concomitant effect on the
257 carbon cycle in forests.

258 Although they generally do not cause major disturbance events in forested landscapes,
259 wood decay organisms, predominately fungi, play a major role in decomposition and carbon
260 cycling in forests. Dozens of fungal species cause decay or “cull” in millions of trees across
261 North America, many of which remain standing, live or dead, for several years to many decades.
262 In southeast Alaska alone it is estimated that >30% of the volume in living, old-growth Sitka
263 spruce (*Picea sitchensis* (Bong.) Carrière) and western hemlock (*Tsuga heterophylla* (Raf.)
264 Sarg.) trees is cull [*Farr et al., 1976*]. Wood decay fungi may also have different roles in carbon
265 cycling: brown rot fungi, which leave behind decay high in lignin and recalcitrant to further
266 breakdown, may contribute to more storage of carbon in forests than do white rot fungi, which
267 progressively digest all wood components, including lignin.

268 Invasive pathogens tend to have more pronounced acute impacts than native species, and,
269 when considered with invasive insects, pose a greater threat to forest ecosystems than do all
270 other non-invasive species combined [*Lovett et al., 2006*]. Indeed, invasive pathogens are

responsible for some of the most significant long-term changes to North American forests that have been observed, including the functional extinction of a number of keystone taxa across all or most of their range.

3. Drivers of biotic disturbances

Several different types of factors act to initiate, maintain, and terminate outbreaks of insects and pathogens, including climate/weather, predators/pathogens, and host plant condition (stressed versus healthy). Below we discuss the major drivers and their effects on the different biotic disturbance agents.

3.1 Drivers that directly affect insects and pathogens

Temperature is a major driver of both insect and pathogen outbreaks, and operates in multiple ways. For insects, life stage development rates increase with temperature, potentially leading to a switch from two- or three-year life cycles (“semi-voltinism”) to one-year life cycles (“univoltinism”), resulting in faster population growth [Bentz *et al.*, 1991; Bentz *et al.*, 2001]. Some insects such as mountain pine beetle are under direct temperature control, facilitating the ability of the insect to take advantage of warmer conditions through more rapid development. Such control also leads to population synchrony for mass attack, often required to overcome tree defenses [Raffa and Berryman, 1987]. Other insects undergo an intrinsic resting state called diapause, which is triggered by low temperatures or shortened photoperiod and acts to maintain

beetle populations in life stages most suited for withstanding cold conditions [Tauber *et al.*, 1986].

Winter temperatures also govern population levels of insects through mortality of overwintering life stages in cold conditions. In response, some insects have evolved the capacity to increase cold-tolerance as the winter progresses [Wygant, 1940]. This cold-hardening offers protection at low temperatures, though populations are still vulnerable to extremely cold winter conditions as well as low temperatures during late fall or early spring when cold-hardening is not present [Régnière and Bentz, 2007].

Pathogens similarly require temperatures above a minimum to grow and survive. However, pathogens are more directly affected by moisture [Desprez-Loustau *et al.*, 2006]. Several pathogens require a minimum continuous time of wet conditions for infection to take place, and for most pathogens, moisture is necessary for reproduction and dispersal [Agrios, 2005].

Disease epidemics are more likely to occur when host susceptibility or pathogen virulence increases, as environmental conditions approach optimum for pathogen growth, reproduction and spread, and as the duration of all conditions favorable to the pathogen is prolonged or repeated [Agrios, 2005]. Virulent pathogens are able to infect hosts quickly to ensure higher amounts of inoculum (= high inoculum potential) and thus disease. Pathogens producing inoculum on aerial parts of hosts are often quickly disseminated by wind and can be dispersed several km [Agrios, 2005]. Pathogens reproducing inside hosts and those that are soilborne and rootborne tend to spread more slowly than airborne pathogens.

Biotic interactions also affect insect/pathogen populations. Predators and pathogens of biotic agents reduce population levels. For the most important bark beetle species discussed in

this review (e.g., mountain pine beetle, spruce beetle), these factors are more important at lower, background population levels. When bark beetle populations are at epidemic levels, the effects of predators and pathogens are greatly reduced [Turchin *et al.*, 1999]. In contrast, defoliators are affected by these factors even during outbreaks [Hajek, 1999; Quayle *et al.*, 2003; Régnière and Nealis, 2007]. In addition to predation, competition can affect populations. For example, wood borers can reduce bark beetle populations through competition for food resources and facultative predation, potentially reducing the likelihood of a transition from background levels to an epidemic [Dodds *et al.*, 2001].

3.2 Drivers that affect insects and pathogens indirectly

Another major driver of outbreaks is the condition of potential host trees. Most insects and pathogens have one or more preferred host tree species, and so forest species composition determines the extent of a potential outbreak. Outbreaks occurring over large areas require large areas of suitable and susceptible hosts. Host age can play a role, with some insects or pathogens preferring younger hosts, others older hosts. Bark beetles prefer larger-diameter trees that provide more food resource [Shore and Safranyik, 1992]. For pathogens and to a lesser-known extent insects, the degree of genetic uniformity of hosts is an important factor: the higher the degree of uniformity, the greater the likelihood of an epidemic. Diseases of long-lived host plants such as trees usually take longer to develop than those of annual crops.

Some insects and pathogens prefer or have easier access to stressed or low vigor trees, which may be less well defended against attack [Raffa *et al.*, 2008]. Hosts predisposed to attack by drought, defoliation, or other stresses often lead to population increase of bark beetles and

latent pathogens. Older trees can be less vigorous and are less able to defend themselves. High-density stands with resultant increased competition for resources, reduced soil fertility, and severe drought can lead to stressed individuals and reduced resistance. Such relationships are not universal, however. For example, folivorous insects generally perform equally well on vigorous and stressed trees. Some insects prefer healthy trees for their superior nutritional content. For example, some sap feeding and shoot feeding insects typically perform better on healthy trees [Koricheva *et al.*, 1998]. Likewise, pathogens show complex and species-specific relationships with host stress. In addition to resistance effects, a tree's ability to tolerate a given amount of feeding or infection often declines with increasing stress.

Host phenological synchrony and nitrogen availability are particularly important for defoliators [Régnière and Nealis, 2007]. Early-season foliage tends to be more succulent and lower in defensive compounds than later-season foliage. Many herbivores are nitrogen-limited, so any factor that increases available foliar nitrogen may shorten insect development time, increase survival, and enhance fecundity.

3.3 Outbreak collapse

Outbreaks of insects and pathogens collapse for varying reasons. Within stands or in extensive outbreaks that occur over large areas, outbreaks can collapse from lack of available remaining food resources [Safranyik and Carroll, 2006a]. Natural enemies play important roles in the population dynamics of folivores [Elkinton and Liebhold, 1990; Régnière and Nealis, 2007], which are more exposed than internally feeding insects such as bark beetles. A common trend is for generalist predators such as birds, small mammals, and spiders to constrain low

populations, but once an outbreak commences, these generalists often lack the reproductive capability to respond, and so parasitic insects and entomopathogens become more important. Weather factors such as extremely cold winters [Safranyik and Linton, 1991] or low year-round temperatures [Logan and Powell, in press] can lead to outbreak collapse.

3.4 Human influences

Anthropogenic emissions of greenhouse gases have resulted in a warming climate that has facilitated outbreaks [Carroll *et al.*, 2004; Logan *et al.*, 2003], and future patterns of insect and pathogen infestations are likely to change in response to projected climate change [Bentz *et al.*, 2010; Hicke *et al.*, 2006; Kliejunas *et al.*, 2009]. Management activities that include selective harvesting, fire suppression, and use of pesticides have led to older, denser stands and/or stands with a higher percentage of host tree species in some forest types, increasing susceptibility to attack by insects and pathogens [Anderson *et al.*, 1987; Blais, 1983; Taylor and Carroll, 2004]. Other forest management practices such as planting even-aged monocultures have led to higher incidences of insect and pathogen outbreaks [Jactel and Brockerhoff, 2007]. The increase in commerce has resulted in increases in invasions by exotic insects and pathogens.

The ability of humans to control epidemics once started varies among insect and pathogen species. Some groups such as bark beetles and most invasive pathogens are effectively immune to human control during epidemics except at a very limited scale such as by treatment of high-value trees with pesticides. Populations of other insect and pathogen species causing defoliation can be controlled by aerial spraying of microbial or synthetic pesticides [Carisey *et al.*, 2004; Johnson *et al.*, 2003; Van Frankenhuyzen, 2000]. Silvicultural practices can modify

forest stand densities, species composition, size classes, and risk of fungal infection (e.g., sterilizing cut stump surfaces) that affect tree vigor and resistance to attack by biotic agents [Durall *et al.*, 2005; Fettig *et al.*, 2007].

4. Disturbance interactions

Insect or pathogen impacts are best understood within the context of interactions with other biotic and abiotic agents. For example, root pathogens, root herbivores, and defoliators can predispose trees to attack by bark beetles and wood borers, and defoliators can release latent pathogens such as some species of *Armillaria*. Insects are frequently the vectors for pathogen dispersal, e.g., symbioses between fungi (*Ophiostoma montium* (Rumbold) von Arx, *Grosmannia clavigera*) and *Dendroctonus* bark beetles [Bleiker and Six, 2007], while conversely trees whose defenses are compromised by pathogens or fire also become more susceptible to insects [Klepzig *et al.*, 1995; Lombardero *et al.*, 2006]. Complex biotic interactions can strongly affect the resilience of forest ecosystems to herbivory. For example, whitebark pine (*Pinus albicaulis* Engelm.) faces the combined and interacting threats of mountain pine beetle and white pine blister rust, which affects all age categories [Six and Adams, 2007]. Outbreaks of forest tent caterpillar or gypsy moth in oak stands are susceptible to subsequent lethal colonization by two-lined chestnut borer (*Agrilus bilineatus* (Weber)).

Insect and pathogens interact with drought and heat to affect forest carbon cycling. A recent global assessment showed that over the past few decades there has been a significant, increasing trend in reporting of drought- and heat-related forest die-off events, including numerous events where biotic agents played either a primary or secondary role [Allen *et al.*,

2010]. Biotic disturbances and interaction have also be suggested as potential causes of increased background tree mortality rates [*van Mantgem et al.*, 2009]. Trees suffering from drought or other abiotic stress generally have a higher likelihood of infection by pathogens, even though drought generally has a negative effect on most pathogens [*Desprez-Loustau et al.*, 2006].

Insects and pathogens interact with other abiotic disturbances as well. Infestations interact with wildfire in two ways [*Jenkins et al.*, 2008; *Parker et al.*, 2006; *Romme et al.*, 2006]. First, outbreaks kill trees, which modifies fuel and fire hazard in complex patterns that vary with time since outbreak [e.g., *Jenkins et al.*, 2008]. However, changes to fire probability or behavior is less well known [*Bentz et al.*, 2009]. Second, fires may affect the likelihood and severity of insect and pathogen outbreaks by altering species composition or stand structure in the long term and by injuring surviving trees in the short term. Large, stand-replacing fires in some areas of North America historically produced landscapes dominated by forests of similar age, structure, and host susceptibility that favor higher outbreak severity and larger extent. Trees that are damaged by fire but still alive become stressed, resulting in a predisposition to secondary host infection that can contribute to physiological weakening, reduced growth rates, and mortality. Empirical studies suggest that insect attack rates are often higher on fire-injured trees, though the strength of these effects varies by insect species, even within a feeding group [*Simard et al.*, 2008]. In addition to fire, interactions occur between biotic disturbances and wind. Nonhost tree species may be more exposed to wind during large-scale defoliator outbreaks. Pathogens can also increase the risk of wind damage by weakening stems or roots [*Papaik et al.*, 2005].

5. Impacts on carbon cycling

Various terms are used to describe carbon cycling. *Carbon stocks* (units of g C or g C m⁻²) are reservoirs of carbon in various tree and soil pools, such as stem, foliage, roots, and organic matter. *Carbon fluxes* (g C m⁻² year⁻¹) are transfers between stocks; here, we focus principally on exchanges between the atmosphere and either vegetation or soil. *Gross primary production* (GPP) is the total amount of atmospheric C fixed by plants. *Autotrophic respiration* (R_a) releases C to the atmosphere by the plants themselves; *heterotrophic respiration* (R_h) is C released by microbes through the decomposition process. *Net primary production* (NPP) is GPP – R_a, and represents the net amount of carbon fixed by plants and available for subsequent use by heterotrophs. *Net ecosystem production* (NEP) is NPP – R_h and defined as positive when ecosystems are sinks of C. *Net ecosystem exchange* (NEE) is the exchange of carbon between the ecosystem and the atmosphere, is defined as positive when there is a net transfer of C to the atmosphere, and is often the same as (but opposite in sign to) NEP. *Net biome production* (NBP) includes NEP as well as losses of C through such processes as combustion or leaching. Chapin *et al.* [2006] describe the differences between these fluxes in greater detail.

5.1 Expected responses of terrestrial carbon cycle to biotic disturbances

Effects of insect and pathogen outbreaks on forest carbon cycling vary with biotic disturbance and host species, forest ecosystem type, and severity of outbreak, but general patterns regarding these interactions exist, based in part on understanding of forest processes following disturbances [Fleming *et al.*, 2002; Hicke *et al.*, 2003; Kashian *et al.*, 2006; Litvak *et*

453 *al.*, 2003; *Odum*, 1969] (Figure 2). First, biotic disturbances alter the productivity (GPP) of
454 stands through defoliation or other growth reductions or tree mortality. Impacts on productivity
455 may be positive or negative depending on the severity of the outbreak and time since the
456 disturbance, though for large-scale outbreaks, short-term effects are typically negative.

457 Second, trees killed by biotic disturbances alter carbon cycling through increases in
458 heterotrophic respiration (decomposition). Carbon in more labile structures such as leaves is
459 released to the atmosphere first, although in killed conifers, needles remain on the dead trees for
460 1-3 years following bark beetle attack, delaying this decomposition. During outbreaks,
461 defoliators consume C in leaves and release large fluxes of nitrogen, carbon, and other nutrients
462 into forest ecosystems through leaf fragments, frass, and exuviae [*Frost and Hunter*, 2004].
463 Snags may remain standing for decades following tree death [*Mitchell and Preisler*, 1998],
464 further delaying decomposition. As a result of these processes as well as the long decay time of
465 wood, the release of carbon through R_h following disturbance occurs over a period of decades to
466 centuries.

467 Reductions in plant productivity (NPP) and increases in decomposition of dead organic
468 matter (R_h) result in large reductions of NEP. The amount of change of these individual fluxes
469 and therefore of the net carbon flux is determined by the magnitude of an outbreak's impact on
470 stands. For severe outbreaks, the magnitude of the effect is large enough to cause a stand to
471 switch from a carbon sink to a carbon source in a manner similar to the effects of wildfire
472 [*Fleming et al.*, 2002].

473 Responses of the carbon cycle are highly dependent on type of biotic disturbance.
474 Several examples illustrate this point. A short-term (e.g., one month) outbreak of a defoliator
475 may have a large but short-lived impact on carbon fluxes. A bark beetle epidemic can kill many

476 trees within a stand within one year, having large and long-lasting effects on carbon budgets.
477 Pathogen and defoliator epidemics that occur over several years before killing a tree can have a
478 large, long-lived effect that is more muted than the bark beetle example. Variability in C cycle
479 responses occurs not only at the tree level but also at the stand level, where the number of trees
480 affected and length of outbreak are important factors.

481 Insect and pathogen outbreaks exert a number of indirect effects on carbon cycling as
482 well. Perhaps most importantly, moderate to severe outbreaks may alter functional attributes of
483 the ecosystem (e.g., light regime, water availability and loss, nutrient cycling) in a way that
484 affects the trajectory of succession and recovery. Outbreaks severe enough to alter soil moisture
485 and nutrients, for example, cause changes in tree density or species composition such that long-
486 term carbon storage or the rate of carbon cycling is also altered. At longer and broader scales,
487 carbon loss to the atmosphere from severe outbreak areas may drive climate feedbacks that could
488 alter the frequency and severity of future insect or pathogen outbreaks. Finally, killed trees
489 resulting from insect and pathogen outbreaks may interact with other disturbances to affect
490 carbon cycling, particularly with fire and wind damage (see discussion above).

491 There is increasing evidence that invasive insect and pathogen outbreaks may have a
492 large impact on forest carbon cycling because of their effects on disturbance regimes, nutrient
493 cycling, and other processes in ecosystems with which they have not co-evolved [*Peltzer et al.*,
494 2010].

495 Biotic disturbances that cause extensive tree mortality may be comparable to fires in
496 terms of impacts to carbon budgets [*Fleming et al.*, 2002; *Kashian et al.*, 2006]. Many biotic
497 disturbances have less immediate impacts than fires, such as defoliation events that kill trees
498 only after several consecutive years of attack [*Fleming et al.*, 2002]. Other outbreaks, such as

those of some bark beetles, can kill many trees within a stand within one year, acting more similar to fire. Differences exist, however: fires result in an immediate release of some carbon to the atmosphere via combustion; severe fires kill nonhost species, understory trees, shrubs, and herbs in addition to host trees; and although outbreaks modify some soil properties such as biogeochemical cycling [e.g., *le Mellec and Michalzik*, 2008; *Morehouse et al.*, 2008], fires can also cause microbial mortality through heating, increase weathering rates, reduce surface albedo, and affect infiltration and runoff rates [*Neary et al.*, 2005].

5.2 Documented impacts of insects and disease on forest carbon cycling

Relatively few studies have quantified the impacts of insect and disease outbreaks on forest carbon budgets. To facilitate comparison, these studies were summarized by insects (Table 3) and pathogens (Table 4). For summarizing and comparing studies, key factors included the type of insect or pathogen (especially whether or not the damage agent killed trees); the severity of disturbance in terms of the number of trees attacked within a stand and the amount of tree mortality; the time since disturbance; the methods of the study and the carbon variable(s) studied; and the existence and type of study controls that illustrate effects relative to unaffected stands or preoutbreak conditions.

We identified 16 studies that assess impacts to North American carbon cycling by insect outbreaks (Table 3) and four studies that documented impacts by pathogens (Table 4). The insect studies were roughly divided among bark beetles, defoliators, and hemlock woolly adelgid, a fluid feeder. Multiple studies of mountain pine beetle, spruce budworm, forest tent caterpillar, gypsy moth, and hemlock woolly adelgid have been published.

Most studies were field observations of carbon cycling [Forrester *et al.*, 2003; Jenkins *et al.*, 1999; Kizlinski *et al.*, 2002; Morehouse *et al.*, 2008; Nuckolls *et al.*, 2009; Pfeifer *et al.*, 2010; Romme *et al.*, 1986], including eddy flux tower measurements [Brown *et al.*, 2010; Clark *et al.*, 2009; Cook *et al.*, 2008; Hadley *et al.*, 2008]. As such, there was an emphasis among studies of tree- to stand-scales. Analyses of eddy flux tower observations were opportunistic (i.e., unplanned), although in one study sites were selected specifically to investigate mountain pine beetle impacts [Brown *et al.*, 2010]. The pathogen studies addressed needle to plot scales.

Several studies used carbon cycle models informed by or parameterized with field observations and concentrated on recent times since outbreak [Cook *et al.*, 2008; Schäfer *et al.*, 2009]. A few studies estimated regional impacts using upscaling of finer scale results, simulation modeling, or remote sensing [Albani *et al.*, 2010; Clark *et al.*, 2009; Dymond *et al.*, 2010; Hicke *et al.*, 2002; Kurz and Apps, 1999; Kurz *et al.*, 2008a], and several assessed effects on time scales of decades to centuries [Dymond *et al.*, 2010; Hogg, 1999; Kurz and Apps, 1999; Kurz *et al.*, 2008a; Pfeifer *et al.*, 2010]. Only one study considered the effects of multiple species [Kurz and Apps, 1999].

Insect and pathogens typically caused reductions in tree- and stand-level NPP immediately following attack [Clark *et al.*, 2009; Cook *et al.*, 2008; Dymond *et al.*, 2010; Hogg, 1999; Manter *et al.*, 2003; Meinzer *et al.*, 2004; Pfeifer *et al.*, 2010; Romme *et al.*, 1986; Schäfer *et al.*, 2009], although one study of beech bark disease reported no change in aboveground NPP across a gradient of impact [Hancock *et al.*, 2008]. Following a disturbance, NEP decreased from large positive values (strong C sinks) to weaker positive values or switched to negative NEP values (C sources) [Albani *et al.*, 2010; Brown *et al.*, 2010; Clark *et al.*, 2009; Cook *et al.*, 2008; Dymond *et al.*, 2010; Kurz and Apps, 1999; Kurz *et al.*, 2008a]. Variability in NEP

reduction was related to the number of trees affected by defoliation or mortality, amount of leaf area reduced by defoliation, and contribution of the understory to carbon uptake. These patterns of NEP change occurred at local scales as well as regional scales during extensive tree mortality. Studies were inconsistent in their conclusions about soil and forest floor carbon impacts, with some noting modified carbon stocks, C:N values, and soil CO₂ efflux in infested stands compared with uninfested stands [Hancock *et al.*, 2008; Kizlinski *et al.*, 2002; Nuckolls *et al.*, 2009], and some reporting no change in one or more variables [Jenkins *et al.*, 1999; Kizlinski *et al.*, 2002; Morehouse *et al.*, 2008].

Fewer studies assessed recovery and long-term impacts. Transient (one year) defoliation resulted in recovery of NEP in the year after the outbreak [Cook *et al.*, 2008]. In contrast, the effects on NPP and NEP from tree mortality following bark beetle outbreaks or repeated defoliation persist longer [Kurz and Apps, 1999; Kurz *et al.*, 2008a; Pfeifer *et al.*, 2010]. Regionally, simulated NEP in a region of an extended outbreak of mountain pine beetle remained a net carbon source for the study period of two decades [Kurz *et al.*, 2008a], and a simulated spruce budworm epidemic affected NEP for over a decade [Dymond *et al.*, 2010]. Localized studies indicated rapid recovery of aboveground carbon stocks or NPP to preoutbreak values or uninfested stands within one to several decades [Forrester *et al.*, 2003; Pfeifer *et al.*, 2010; Romme *et al.*, 1986]. Several decades following an outbreak, stand productivity may be higher than preoutbreak values because the growth of surviving trees accelerates after release from competition [Romme *et al.*, 1986], although this pattern did not occur in simulated NPP recovery following an outbreak in a different area [Pfeifer *et al.*, 2010]. The speed and magnitude of the recovery of productivity depend on the severity of the outbreak (number of trees affected), composition of the surviving trees within the stand, and seedling establishment

rate [Pfeifer *et al.*, 2010].

Several studies noted some of the regional forest management implications of bark beetle outbreaks. Kurz *et al.* [2008b] described the significant implications of the 1990 baseline used by the UN Framework Convention on Climate Change for forest carbon stocks, a time when Canadian insect outbreaks were minimal, compared with inventory and models suggesting that the trajectory of Canadian insect outbreaks under climate change and land management may approach 30% of fossil fuel emissions. Using simulation modeling, Seidl *et al.* [2008] show that the interaction of European spruce bark beetle (*Ips typographus* L.) outbreak severity and climate change strongly modifies future carbon stocks of central European Norway spruce (*Picea abies* (L.) Karst.) forests.

Although the focus of this paper is on North America, we include a brief discussion on the few relevant studies outside of this region. Studies of short-term carbon cycling impacts based on eddy flux tower observations reported reductions in photosynthesis and NEP for sap-sucking [Kirschbaum *et al.*, 2007] and defoliating [Allard *et al.*, 2008] insects. Carbon fluxes to the soil and C:N ratios in frass were greatly increased in areas attacked by pine lappet moth (*Dendrolimus pini* L.) [le Mellec and Michalzik, 2008; le Mellec *et al.*, 2009], and experiments of the effects of a fungal pathogen found reduced plant productivity following infection [Luque *et al.*, 1999]. These few findings from studies in Europe and Australia are consistent with those in North America.

6. Knowledge gaps

Our review of published studies indicates substantial gaps in knowledge. A clear need is *additional scientific understanding of a broader range of biotic disturbance agent types*. The natural history, ecology, and population drivers of only a few insects and pathogens (i.e., those of historical importance) have been studied. Moreover, even for the best-studied insects (e.g., mountain pine beetle), we lack sufficient knowledge about drivers to build robust predictive models of population dynamics important for carbon cycle studies, and some of the better-understood drivers are rapidly changing with a variety of anthropogenic conditions. Less is known about most pathogens, and biotic disturbance agents in some North American regions (especially Mexico) are little understood though may be quite important [Salinas-Moreno *et al.*, 2010].

In addition to natural history, we *lack quantitative understanding of the spatial and temporal characteristics of insect and pathogen outbreaks*. Aerial surveys are undertaken annually in the US and Canada to provide information about general trends and are rich in spatial, temporal, and attribute information. However, these data sets have limitations as noted below in Section 7.2. Even if impact areas were well known, *uncertainties exist on how to convert area or number of affected trees to metrics important for carbon cycle studies* (e.g., leaf area or carbon pools). For insects and pathogens that do not kill trees, identification of impacts to carbon cycling based on affected area is very difficult because these disturbances often progress slowly, making detection difficult, and we lack much understanding of effects of these agents on trees.

For most species, we lack knowledge of life history traits and drivers that can be used as a basis for predictive modeling. For those insects and pathogens for which we have such knowledge, additional research is needed to integrate insect/pathogen responses with host responses as well as to evaluate predictions. In addition, our *predictive capability of invasions by exotic insects and pathogens is limited*. Invasions may take the form of range expansion into formerly unoccupied habitat or successful introductions of exotic species. Each has the potential to exert large impacts to carbon stocks and fluxes, yet our ability to estimate when, where, and in which host species invasions will occur is very limited.

General conclusions about C cycle processes are subject to *large uncertainty as a result of the lack of replication of studies*. Few studies of impacts on carbon cycling exist, limiting comparisons among studies. Furthermore, replicating impacts of similar insect/pathogen and host type under similar conditions, particularly amount of defoliation and/or mortality and time since disturbance, is challenging. For example, whether a bark beetle-infested stand is a net C source or sink depends on the extent of tree mortality, number and size of surviving trees, spatial pattern of mortality, and time since outbreak, among other processes. Attempts to match conditions among published studies resulted in very few meaningful comparisons (Tables 3 and 4).

The lack of existing C cycle studies implies several gaps in knowledge. The majority of existing studies concern insect outbreaks; *very few studies of impacts of pathogen outbreaks on C cycle* have been reported. Even so, the number of insect species studied is limited to mountain pine beetle, hemlock woolly adelgid, gypsy moth, forest tent caterpillar, and a few other defoliators. *Additional studies are needed to quantify the changes to carbon pools and fluxes associated with different types and severities of outbreaks*. These changes include those from

direct effects, such as loss of GPP, loss of leaf area, changes in plant allocation patterns, and changes in rates of leaf, root, and coarse woody debris inputs to the soil. In addition, studies of indirect effects and ecosystem feedbacks such as changes in microclimate, albedo, heterotrophic respiration, and species composition are needed. The production and decomposition of coarse woody debris is not well characterized. Snagfall rates are important for controlling rates of decomposition, yet little is known about rates and drivers. Seedling establishment is another important yet poorly understood process often following outbreaks. The size and number of surviving trees is key to determining how rapidly postoutbreak NPP increases, yet we have little information about how these factors vary within and among outbreaks. More information is needed about the dynamics of C stocks and fluxes following these disturbances.

Interactions with other disturbances are not well quantified. The interactions between drought and heat stress and biotic disturbances as drivers of tree mortality events are poorly understood. There is currently only limited mechanistic knowledge of the physiological processes and linkages involved [Adams *et al.*, 2009; Breshears *et al.*, 2009; McDowell *et al.*, 2008]. Another feedback loop that has received little attention to date is how large-scale outbreaks of biotic agents might affect such biophysical processes such as leaf area, forest transpiration/stomatal conductance, and albedo [Adams *et al.*, 2010; Bonan, 2002; Hogg *et al.*, 2000]. Modifications to these processes drive changes in surface energy and water budgets, affecting local and regional weather and climate patterns (including amplification of drought and heat stress).

Limited information exists on landscape- to continental-scale impacts on carbon budgets. Effects of major outbreaks of most large-scale insect and pathogen outbreaks have not been studied. In addition to North America, forest dieoff on other continents has been reported, due in

part to biotic disturbance [Allen *et al.*, 2010], suggesting major modifications to carbon budgets in these other regions.

Biotic disturbances are missing from many carbon cycle models. Possible model modifications to include these disturbances may range from simple (fractional removal of carbon pools as a function of biotic outbreak drivers) to statistical (probability based stochastic outbreaks) to predictive, dynamic (coupling biotic population models to carbon cycle models) changes. Key challenges remain in conceptualizing the level of complexity needed to accurately constrain carbon budget impacts from insect and pathogen outbreaks.

7. Available tools

7.1 Field observations

Methods and tools available for understanding processes associated with carbon cycle impacts using field observations are well established. Techniques to measure carbon stocks and fluxes with field equipment have been widely applied. Similarly, carbon budgets using measurements from eddy flux towers are well understood. One issue that arises in some regions is that forests and their biotic disturbances occur in complex terrain. Such terrain induces advective air flows within and above the canopy that may pose significant challenges for interpreting results from eddy flux towers [Sun *et al.*, 2010]. In addition, flux tower data are spatially integrative, leading to challenges of differentiating effects of variations in outbreak severity that may occur within their spatial footprint.

Ground surveys and pheromone trapping are critical for providing precise information regarding field conditions. Surveys allow for the identification of specific insects or diseases, collection of samples for further analysis (e.g., genomic/molecular characterization, tree defense chemistry), assessment of wood damage/growth reduction, the persistence of reservoir populations at levels not detectable by other means, and early detection of the incidence or population increase of most pathogens and insects. The limitations of ground surveys are their cost, personnel, and difficulty of capturing fine-scale, patch patterns across large spatial scales through point sampling. However, some networks such as the USDA Forest Service Forest Inventory and Analysis (FIA) program or the Canadian Forest Inventory (CanFI) may provide the ability to assess changes to carbon budgets following outbreaks [Thompson, 2009a; Thompson, 2009b]. Additional relevant information such as disease is collected on a subset of the FIA plots. The Mexican CONAFOR (Comisión Nacional Forestal) is currently in the planning stages for a forest health survey (B. Tkacz, pers. comm.).

Several notable challenges exist when using field observations. Biotic disturbances are relatively sparse in time and space, and we currently lack the capability to generate accurate short-term predictions of these disturbances at local spatial scales. This inability to forecast outbreaks suggests difficulty in setting up studies in advance of a disturbance. Establishing a control for comparison of effects is also a challenge, whether in time (forecasting an outbreak to obtain pre-outbreak measurements) or space (finding similar stands and environmental conditions). Developing chronosequences of time since disturbance that substitute space for time requires identification of similar stands with similar levels of impact across decades, yet identifying old stands becomes more difficult as the biotic disturbance evidence fades with time.

7.2 Aerial survey databases

The detection, mapping, and monitoring of the spatial location, areal extent, and severity of forest disturbances have been long-standing activities in North America [Tkacz *et al.*, 2008]. Aerial surveys are important tools and consist of trained observers delineating damaged areas from aircraft and estimating disturbance severity, host type, and causal agent [Ciesla, 2000; McConnell *et al.*, 2000]. In the United States, the annual Aerial Detection Survey program is undertaken in collaboration with various state and federal agencies, with regional data available from 1997 to the present and subsets available further back in time [e.g., USDA Forest Service, 2009c]. In Canada, the Forest Insect and Disease Survey of the Canadian Forest Service conducted annual surveys [Hall *et al.*, 1998] until 1996, when surveys largely became the responsibility of provincial and territorial governments.

Historical and current survey maps can contain limitations that make comparisons problematic, including its subjective nature and range of spatial precision [de Beurs and Townsend, 2008; Harris and Dawson, 1979; McConnell *et al.*, 2000]. Furthermore, spatial and temporal extents are limited. In Canada, aerial surveys are largely confined to managed forests, resulting in an omission of damage information in remote areas, and are limited to the extent that they can be used alone to relate defoliated areas to impact [MacLean, 1990]. In the US, surveys were historically limited to timber-producing tree species and did not include national parks or wilderness areas. Aerial surveys include live trees within damage polygons, and this “affected area” is an overestimate of the area of mortality. Approaches to address this problem include deflation factors to convert the affected area to area of tree mortality [Kurz and Apps, 1999] as

well as combining aerial survey information with remotely sensed imagery to identify the specific area in which the disturbance has taken place [Rogan *et al.*, 2006].

Aerial surveys have two additional important limitations. First, they are generally ineffective for identifying outbreaks of most pathogens, except in cases where a single agent damages large patches of one dominant host species that responds with a distinct foliar pathology. Unfortunately, the patchy, discontinuous nature of disease occurrence associated with many native pathogens makes their distribution and severity very difficult to accurately assess from the air. For example, Morrison *et al.* [2000] found incidence of *Armillaria* root disease to be significantly higher than indicated by aboveground symptoms only. Secondly, aerial surveys typically cannot detect signals of insect activity until key thresholds separating different population phases have already been breached [Safranyik and Carroll, 2006b], and so have limited utility for studying sub-outbreak dynamics or underlying mechanisms of transition.

7.3 Satellite imagery

There is a long history in using remotely sensed satellite imagery for assessing insect outbreaks in forest canopies. Medium-resolution (30-80 m) satellite images have been used to assess defoliation caused by a range of species, including forest tent caterpillar [Hall *et al.*, 2003; Hall *et al.*, 2006], gypsy moth [Nelson, 1983; Williams and Nelson, 1986], spruce budworm [Franklin and Raske, 1994; Leckie and Ostaff, 1988], mountain pine beetle [Franklin *et al.*, 2003; Wulder *et al.*, 2006], jack pine budworm (*Choristoneura pinus*) [Hopkins *et al.*, 1988; Radeloff *et al.*, 1999], and hemlock wooly adelgid [Royle and Lathrop, 1997]. Reasonably accurate satellite image classification results have been obtained by classifying single images

[e.g., *Ahern*, 1988; *Radeloff et al.*, 1999] as well as by assessing interannual spectral changes using multi-temporal data sets [e.g., *Goodwin et al.*, 2008; *Vogelmann et al.*, 2009].

Several key characteristics determine the usefulness of satellite imagery for quantifying outbreaks. Spatial resolution is important: smaller outbreaks can be detected using data from high spatial resolution sensors (2-4 m), such as IKONOS or QuickBird [*Coops et al.*, 2006; *Hicke and Logan*, 2009]. Many studies have used medium-resolution imagery (~30 m, such as Landsat) [*Hall et al.*, 2006; *Vogelmann et al.*, 2009; *Wulder et al.*, 2006], and more recent studies of large outbreaks included coarse-resolution imagery such as Systeme Pour l'Observation de la Terre (SPOT) VEGETATION [*Fraser and Latifovic*, 2005] or Moderate Resolution Imaging Spectroradiometer (MODIS) [*Coops et al.*, 2009; *de Beurs and Townsend*, 2008]. Addressing the significant knowledge gap of quantifying the extent of biotic disturbances will require medium- and coarse-resolution imagery that sense much larger spatial extents and are much less expensive than high-resolution alternatives.

Temporal resolution is coupled with spatial resolution: higher spatial resolution typically means longer repeat times, whereas coarse-resolution MODIS imagery is available twice daily. Repeat intervals are less important for tree mortality events, but are more important for capturing potentially short-lived defoliation events at the specific time when the physical discoloration or loss of foliage is most visible for detection.

The location of spectral bands is important, although most sensors provide imagery in visible and near-infrared wavelengths useful for mapping tree mortality. Hyperspectral remote sensing appears to be a promising technology for the detection of pathogens because it is able to detect plant stress far in advance of actual defoliation [*Govender et al.*, 2008], quantify fine-scale

patchy damage patterns [*Hatala et al.*, 2010; *Pu et al.*, 2008], and even detect root disease [*Leckie et al.*, 2004].

Aside from sensor characteristics, a multitude of algorithms and approaches ranging from classification to modeling have been used to assess damage from insect defoliators and bark beetles [*Hall et al.*, 2006; *Wulder et al.*, 2006]. The combination of sensor and methods of analysis have tended to be species- and site-specific as a result of the wide variation in physiological responses associated with the physical manifestation of damage that ranges from foliage color change to physical loss of foliage.

7.4 Models of insect and pathogen outbreaks

Models of forest pathogens and insects have been developed from a number of different perspectives and with different goals. “Hazard rating” models estimate the susceptibility of a stand to attack based on its structure (age, stem density, etc.) [*Krist et al.*, 2007], and may include simple representations of climate and populations [*Shore and Safranyik*, 1992]. Climate suitability models assess whether conditions are conducive to outbreaks based on temperature and/or drought. Such models can be based on empirical analysis [e.g., *Carroll et al.*, 2004], climate envelop models [e.g., *Magarey et al.*, 2007], or fundamental processes measured in the laboratory [e.g., *Bentz et al.*, 1991]. Neither hazard rating nor climate suitability models predict individual outbreaks, but rather are used to assess current conditions that could potentially lead to outbreaks.

Models of population dynamics, which are often based on spatial extensions of traditional epidemiological models, simulate the course of an epidemic. These models may include such

processes as outbreak initiation, dispersal, and collapse, although some processes may be prescribed by the user instead of simulated [e.g., *Beukema et al.*, 1997; *Cairns et al.*, 2008; *Logan et al.*, 1998]. Biotic interactions between host and insect/pathogen are not present in hazard rating or climate suitability models but are included in population dynamics models. For example, grid-based models have been used to scale single plant studies to populations [Kleczkowski *et al.*, 1997] and to assess the potential role of pathogens in facilitating plant migration through enemy release [Moorcroft *et al.*, 2006]. Newer Bayesian population models show promise for data-driven assessments of disease population dynamics that can account for multiple data sources and the uncertainty associated with the often indirect evidence for pathogen abundance [Hatala *et al.*, in press].

A number of detailed modules for specific insects, pathogens, or functional groups have been developed for the US Forest Service's Forest Vegetation Simulator (FVS), a forestry-oriented stand simulator [Beukema *et al.*, 1997; Frankel, 1998; Hagle *et al.*, 1995; Hansen and Goheen, 2000; Robinson and Geils, 2006]. Similar modules have been developed for the British Columbia Ministry of Forests' Tree and Stand Simulator (TASS), such as the Canadian Forest Service's Root Rot Simulator (ROTSIM), originally developed for laminated root rot (*Phellinus weirii* (Murrill) R.L. Gibertson) in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) [Bloomberg, 1988] and recently adapted for Armillaria root disease [Morrison, 2005]. Detailed “stand-alone” forest pathogen simulators also exist, such as the “Root Rot Tracker” model of forest root diseases [Peet and Hunt, 2005]. For large regional assessments, mechanistic models of pathogen dispersal have been developed that account for both wind characteristics on a continental scale and environmental determinants of spore viability (relative humidity, temperature, UV-B radiation) [Aylor, 2003].

Variability in drivers across species or groups of species implies that modeling outbreaks of biotic disturbance agents requires understanding the natural history of each individual species, or at a minimum, functional groups of similar species. For a limited number of economically important insect species such as mountain pine beetle, spruce budworm, or gypsy moth, predictive models have been developed either empirically or through laboratory studies [Hansen *et al.*, 2001; Logan *et al.*, 2003]. These models usually predict one specific driver (e.g., probability that a given winter's temperatures will result in insect mortality). In one case, mountain pine beetle, models exist for most important drivers, including winter mortality, year-round temperature control of life stage development rates, and host susceptibility [Carroll *et al.*, 2004; Logan and Bentz, 1999; Logan and Powell, 2001; Régnière and Bentz, 2007; Shore and Safranyik, 1992], but limited predictive capability exists for the vast majority of insects and pathogens. Full integration of stand conditions, climate suitability, population dynamics, and host/biotic disturbance agent interactions that allow for more complete simulations have yet to be accomplished.

7.5 Models of the carbon cycle

Models of the carbon cycle often include wildfire and harvest disturbances, but few include biotic disturbance agents. Exceptions include studies of the role of defoliation [Cook *et al.*, 2008], aspen decline [Hogg, 1999; 2001], and tree mortality [Albani *et al.*, 2010; Kurz and Apps, 1999; Kurz *et al.*, 2008a; Pfeifer *et al.*, 2010]. In general, C cycle models are positioned to include biotic disturbances, though challenges remain. In addition to prescribing or predicting the number of trees infested (though an outbreak submodel, for instance), correct simulation

requires understanding how to model response of the carbon cycle to insect or pathogen outbreak in terms tree growth reduction and mortality. Subsequent ecosystem impacts important to carbon cycling such as decomposition, snagfall rate, regeneration, and surviving stand composition also suggest their importance for inclusion in simulations of impacts.

8. Summary and conclusions

Numerous insect and pathogen species impact forests of North America. A few particularly important species affect large areas across many regions, suggesting major impacts to carbon budgets. Life histories of some well-studied species are relatively well understood, but little is known about the majority of important biotic disturbance agents.

Relatively few studies have documented effects of insect or pathogen impacts on stand-level carbon cycling. Tree productivity is reduced in outbreaks, and tree mortality caused by insects or pathogens creates a large amount of dead wood that subsequently decomposes. As a result, NEP is often reduced substantially, sometime switching from a typical sink of carbon to a source. NPP following tree mortality events can recover within a decade or so, though effects on NEP associated with decomposition last longer.

Fewer studies have quantified effects at larger spatial scales. Some of these studies illustrate large impacts on carbon cycling, others more minor impacts, depending on the number of trees affected regionally.

Difficulties arise in obtaining consistency among studies due to several factors. The number of affected trees varies within and among outbreaks of the same species, and impacts (defoliation, growth reduction, mortality) vary among types of disturbance agents. In addition,

time since outbreak is a major determinant of carbon cycling, and different studies have focused on different periods. Future studies of biotic disturbance effects on carbon budgets should include key information that permits comparisons across studies, including spatial and temporal extent of damage, number of trees infested within study region, and time since disturbance. Studies should provide controls for comparison, either preoutbreak and/or in uninfested stands, to quantify the relative magnitude of impact.

Biotic disturbances are often strongly influenced by abiotic factors. Climate change effects on host trees through heat or drought stress are often associated with insect or pathogen outbreaks. Insects and pathogens often interact to affect forest ecosystems. Such interactions make identifying the individual role of biotic agents relative to other potential causal factors difficult, particularly climatic and forest stand condition stressors of forest tree condition. Invasive insects or pathogens have great potential to affect tree species and therefore carbon budgets. We have, however, little capability for predicting invasions, however.

It is clear that biotic disturbances are critical elements of the North American carbon budget, and considerable uncertainties and knowledge gaps exist in our ability to predict or estimate their effects on the carbon cycle. Additional research across a range of disturbance types and spatial and temporal scales is needed to reduce uncertainties of the effects of insect and pathogen outbreaks on carbon cycling.

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1527 Figure Captions

1528

1529 Figure 1. Area affected by major insect species from US and Canadian aerial survey databases.

1530 Example species chosen to illustrate variability among species, through time, and between

1531 regions. “Affected area” includes live and dead trees. Note that impact on carbon cycle varies

1532 across species depending on whether insect is a defoliator (a, b, c, d), which may or may not kill

1533 trees, or tree-killing bark beetles (e, f).

1534

1535 Figure 2. Conceptual diagram showing impacts of insect and pathogen outbreaks on carbon

1536 budgets. Numbers outside of boxes indicate studies in Tables 3 and 4 that provide evidence.

1537 Studies that provide evidence counter to that indicated in diagram noted in bold underlined text

1538 (two cases).

1539

	gypsy moth (<i>Lymantria dispar</i> L.)	multiple trees species throughout northeastern US; primarily angiosperms but also <i>Larix</i> and <i>Pinus strobus</i> L.	invasive	early 1980s: 5.3 Mha, northeastern US ^e ongoing: 600,00 ha, northeastern US ^e	41
	forest tent caterpillar (<i>Malacosoma disstria</i> Hubner)	broadleaf species in North America	native	early 2000s central US: 2.8 Mha ⁱ Canada: 14 Mha ^d	1
fluid feeders	hemlock woolly adelgid (<i>Adelges tsugae</i> Annand)	hemlock (<i>Tsuga</i> spp.)	invasive	ongoing and expanding; in 17 states in eastern US ^e	2
wood borers	emerald ash borer (<i>Agrilus planipennis</i> Fairmaire)	ash spp. (<i>Fraxinus</i> spp.)	invasive	introduced in 2002; ongoing outbreak threatening species extirpations ^j	5
root feeders	weevils (<i>Curculionidae</i> spp.)	maple (<i>Acer</i>), birch (<i>Betula</i>)	invasive	15% of fine root biomass of northern hardwood forests in upper Midwestern US consumed annually ^k	N/A

^aEstimates of basal area loss in the next 15 years for the US [Table 3 in Krist *et al.*, 2007]; similar standardized estimates not available for Canada or Mexico

^bhttp://www.usu.edu/beetle/databases_bark_beetle.htm

^cUSDA Forest Service [2009b]

^dNatural Resources Canada [2009]

^eUSDA Forest Service [2009c]

^fFor southern pine beetle, all acres within a county were counted if that county contained a single infested tree.

^gBreshears *et al.* [2005]

^hCandau *et al.* [1998]

ⁱUSDA Forest Service [2005b]

^jPoland and McCullough [2006]

^kCoyle *et al.* [2008]

Table 2. Pathogens and declines that cause major impacts to the North American carbon budget.

Pathogen type	Disease name (pathogen species)	Host tree species	Origin	Examples of major epidemics and/or long-term perturbations and impacts	US basal area risk ^a (million m ²)
canker	chestnut blight (<i>Cryphonectria parasitica</i> (Murrill) Barr.)	American chestnut (<i>Castanea dentata</i> (Marshall) Borkhausen)	invasive	1920s: 3.5 billion trees infected ^b 1950s: 3.6 Mha dead or dying ^c <i>C. dentata</i> extirpated from its original range ^d	host extirpated
	beech bark disease (<i>Neonectria</i> spp.)	American beech (<i>Fagus grandifolia</i> Ehrh.)	invasive	1970: most of the NE USA and SE Canada affected ^e 1977: Vermont lost 708,000 cubic m ^f	7
foliar	Red band needle blight (<i>Dothistroma septosporum</i>)	pinus (<i>Pinus</i>) and other conifers	native	2002-2004: 38,000 ha impacted, mortality of 2,700 ha in NW BC ^g Extensive mortality in plantations in BC ^h	N/A
	Swiss needle cast (<i>Phaeocryptopus gäumannii</i> (Rohde) Petrak)	Douglas-fir (<i>Pseudotsuga menziesii</i> (Mirb.) Franco)	native	2010: 160,000 ha affected in Oregon ⁱ 2000: stands with the most severe SNC had volume growth loss of approximately 52% ^j	N/A
wilt	Dutch elm disease (<i>Ophiostoma ulmi</i> (Buisman) Nannf and <i>O. novo-ulmi</i>)	elms (<i>Ulmus</i> spp.)	invasive	1930-1973: widespread loss of large trees across NA ^{d,k}	1
root	Armillaria root disease (<i>Armillaria solidipes</i> = <i>A. ostoyae</i>)	mainly conifers	native	responsible for volume losses of 2-3 Mm ³ year ⁻¹ in Canada's Pacific NW ^l in some forests of western NA, 35% of annual tree mortality caused by <i>Armillaria</i> ^m	48 (all root diseases)

Pathogen type	Disease name (pathogen species)	Host tree species	Origin	Examples of major epidemics and/or long-term perturbations and impacts	US basal area risk ^a (million m ²)
	Annosus root disease (<i>Heterobasidion annosum</i> = <i>H. occidentale</i> & <i>H. parviporum</i>)	many conifer and hardwood species	native	infections range from 10-50%; in severe cases 30% of a stand may be killed ⁿ 12.5% of CA commercial forest land is infested, annual losses of 262,000 cubic m ^o	48 (all root diseases)
stem rust	fusiform rust (<i>Cronartium fusiforme</i> Hedgcock & Hunt ex Cummins)	loblolly (<i>P. taeda</i>), slash (<i>P. elliotii</i> var. <i>elliottii</i>) pines	native	1930s: recognized as problem in MS & LA, regionally up to 30% of seedlings infected ^p 1960-70s disease incidence: 5.5 Mha affected >10%, 1 Mha >50% ^{p,q,r}	2
	white pine blister rust (<i>Cronartium ribicola</i> J.C. Fisch Ex. Raben)	Five-needle pines (<i>Pinus</i> spp.)	invasive	in northern Idaho, trees decreased 90% where previously dominant ^s 0.6 Mm ³ estimated mortality loss in Canada, 1976 ^t	2
dwarf mistletoe	<i>Arceuthobium</i> spp.	Pinaceae and Cupressaceae	native	in Canada, 3.5 Mm ³ loss to growth reduction and mortality in 1981 and 1987 ^t in US, 3.8 Mha, 11 Mm ³ (10-50% of annual commercial harvest) lost/year in growth, mortality ^{u,v}	6
Phytophthora	sudden oak death (<i>Phytophthora ramorum</i> sp. nov)	Numerous spp. identified as potential hosts	invasive	1990s: in CA, caused mortality of >3 million oaks (<i>Quercus agrifolia</i> Née) and tanoaks (<i>Lithocarpus densiflorus</i> (Hook. & Arn.) Rehd.) ^w	5
decline	aspen decline (multiple causes including drought, damage by insects and pathogens)	Trembling aspen (<i>Populus tremuloides</i> Michx.)	began recently	2008 mortality in CO forests was > 222,500 ha ^x in Ontario, Canada, area affected >500,000 ha in 2000-2004; plot-level mortality of 74% in 2005 ^y 2000s: mortality across 10 Mha in Saskatchewan and Alberta ^z	6

^aEstimates of basal area loss in the next 15 years for the US [Table 3 in Krist *et al.*, 2007]; similar standardized estimates not available for Canada or Mexico

^bAgrios [2005]

^hWoods *et al.* [2005]

^mSinclair *et al.* [2005]

^sNeuenschwander *et al.* [1999]

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ⁱwww.cof.orst.edu/coops/snc

ⁿLittke and Browning [1989]

^tSingh [1993]

^zHogg *et al.* [2008]

^dLoo [2009]

c/2010Results.htm

^oMarosy and Parmeter [1989]

^uGill [1954]

^eGriffin *et al.* [2003]

^jMainwaring *et al.* [2005]

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^vDrummond [1982]

^fHouston [1994]

^kFarrar [1995]

^qSchmidt *et al.* [1986]

^wGoheen *et al.* [2006]

^gWatt *et al.* [2008]

^lMorrison and Mallet [1996]

^rAnderson *et al.* [1986]

^xUSDA Forest Service [2009a]

Table 3. Summary of studies that report effects of insect outbreaks on carbon budgets.

Outbreak characteristics				Study characteristics					Study results		Reference
Insect type	Insect species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable ^a	Results	
bark beetles 1 ^b	mountain pine beetle	lodge-pole pine	British Columbia	two years of field measurements (eddy flux tower), 2006-2007	two stands, MPB-03 and MPB-06	MPB-03: 4-5 years MPB-06: 0-1 years	>95% red- and gray-attack Year 1: 50% green-attack Year 2: 73% dead	none Year 1, pre-attack	NEP	-56 and 4 g C m ⁻² yr ⁻¹ in Years 1 and 2 -82 and -33 g C m ⁻² yr ⁻¹ in Years 1 and 2	<i>Brown et al.</i> [2010]
2				simulation modeling	regional	21 years during and following outbreak	varies	years prior to outbreak	NBP	NBP change from sink to a source; magnitude of source was reduced but >0 after 21 years	<i>Kurz et al.</i> [2008a]
3			Yellowstone area	field measurements (dendrochronological)	4 attacked stands	decades before, 10-20 years following infestation	41-67%	preoutbreak and uninfested control stands	NPP as indicated by bole volume increment	10 years to recovery to preoutbreak values and values from unattacked stands	<i>Romme et al.</i> [1986]
4			central Idaho	field measurements, simulation modeling	12 stands	100+ years following outbreak	18-52% number of trees, 31-83% C stocks	years prior to outbreak and uninfested control simulations	above-ground C stocks above-ground woody C production	recovered to preoutbreak values in 1-25 years and to unattacked simulations in 56-185 years never recovered to preoutbreak values; recovered to unattacked simulations in 30-160 years	<i>Pfeifer et al.</i> [2010]
5	<i>Ips</i> and <i>Dendroctonus</i>	ponderosa pine	south-western US	field measurements	10 infested	0-2 years following infestation	80%	10 uninfested stands	above-ground C stocks soil respiration	60% in killed trees similar among infested and uninfested stands	<i>Morehouse et al.</i> [2008]
defoliators 6	forest tent caterpillar outbreaks (with drought)	aspen	two sites in central Canada	dendrochronology, simulation modeling	multiple stands	decades before and after outbreak	70% of leaf area lost per tree (prescribed); #trees attacked from tree ring analysis (19-97%)	results in years before and years after outbreak	stem growth stem C	reduction by 80-90% reduction by 15-25%	<i>Hogg</i> [1999]

Outbreak characteristics				Study characteristics					Study results		Reference
Insect type	Insect species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable ^a	Results	
7	forest tent caterpillar outbreaks	north- ern hard- wood	Wisconsin	field measurements, eddy flux tower, simulation modeling	one stand	year of, year before, year after outbreak	40% of leaf area	measurements in year before and year after outbreak	GPP NEP	24% decrease during year of outbreak reduction in sink (77 g C m ² year ⁻¹ vs. 323-422 g C m ² year ⁻¹)	<i>Cook et al.</i> [2008]
8	gypsy moth	pine/ oak	New Jersey	field measurements, eddy flux tower, modeling upsampling using aerial surveys	three stands 1588 km ²	two years during outbreak year of outbreak	partial to complete defoliation in second and third years 20% of landscape had 75% defoliation	year prior to outbreak estimate without outbreak	GPP NEP annual NEE	25-58% reduction reduced sink or switch to C source 41% reduction; 55% reduction in most impacted stands	<i>Clark et al.</i> [2009] and <i>Schäfer et al.</i> [2009]
9	eastern spruce budworm	eastern forests	Canada, US	remote sensing, modeling	regional	5-40 years following defoliation	unspecified	none	NPP	recovery indicated by increasing NPP over 17-year period	<i>Hicke et al.</i> [2002]
10			Quebec, Canada	simulation modeling	regional (106,000 km ²)	outbreak and study period 2011-2024	various: 0-30% mortality per year; 0-86% growth loss per year; 95% of study region experienced defoliation	simulations without outbreak	C stocks NPP NBP	reductions of 11-90% in merchantable C and 2-10% in ecosystem C reduction of 3.5% switch from sink (4.6 g C m ² yr ⁻¹) to source (-16.8 g C m ² yr ⁻¹) during outbreak	<i>Dymond et al.</i> [2010]
11	fluid feeders hemlock woolly adelgid	eastern hemlock species	north-eastern US	eddy flux towers	hemlock and oak stands	N/A; effects estimated by comparing pre- and postoutbreak forest types	N/A; outbreak effects estimated by comparing pre- and postoutbreak forest types	N/A	NEE	maximum postoutbreak forest (oak) uptake 60% greater than hemlock annual NEE similar	<i>Hadley et al.</i> [2008]
12				field measurements	six sites	5-6 years after initial infestation	ranged from 0-98% basal area in infested hemlocks	sites across gradient of damage	soil C and C:N in total soil, forest floor, or mineral soil	no differences among sites with different levels of infestation	<i>Jenkins et al.</i> [1999]

Outbreak characteristics				Study characteristics					Study results		Reference
Insect type	Insect species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable ^a	Results	
13				field measurements	six infested sites	unspecified	43% of hemlock trees killed, 35% of basal area	four control sites	soil C, mineral C:N forest floor mass, forest floor C:N	no differences compared with uninfested stands lower in damaged sites	<i>Kizlinski et al.</i> [2002]
14			southern US	field measurements	plots	three years of infestation	unspecified	year prior to infestation and hardwood plots without infestation	basal area increment very fine root biomass soil CO ₂ efflux	decreased by 50-90% decreased by 20-40% in two years decreased by 20% in one year	<i>Nuckolls et al.</i> [2009]
15			eastern US	spread and ecosystem modeling	hemlock locations in eastern US	continuous	linear increase 0-50% for 0-20 years following initial infestation	simulation without insect outbreak	regional NEP	for 2000-2040 period, reduction by 8%; for 2040-2100 period, increase by 12%	<i>Albani et al.</i> [2010]
multiple 16	eastern spruce budworm, mountain pine beetle, jack pine budworm, hemlock looper	various	Canadian forests	simulation modeling	regional	1920-1989	various	years prior to infestation	NEP	increased disturbance (insect outbreaks, fire) in latter decades contributed to switch from sink to source	<i>Kurz and Apps</i> [1999]

^aSee text for explanation of abbreviations.

^bStudy identifier used in Figure 2.

Table 4. Summary of studies that report effects of pathogen outbreaks on carbon budgets.

Outbreak characteristics				Study characteristics					Results		Reference
Pathogen type	Pathogen species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable ^a	Results	
canker 17 ^b	beech bark disease	American beech	northeastern US	field observations	eight plots	unspecified	5-95% live beech by basal area; no information provided about %beech killed	gradient of beech bark disease damage	above-ground NPP growing season soil CO ₂ efflux	no differences across disease gradient decreased by 40% in infested stands	<i>Hancock et al.</i> [2008]
18				field observations during (1985) and after (2000) outbreak	49 plots	15 years	see biomass	preoutbreak measurements	above-ground live biomass of beech litterfall, % lignin	1% reduction in live and 99% increase in dead beech no change	<i>Forrester et al.</i> [2003]
foliar 19	Swiss needle cast, <i>Phaeocryptopus gaeumannii</i>	Douglas-fir	western Oregon, US	field measurements and modeling	trees at three sites	ongoing	density of pathogen: 0-70% of needle stomata	uninfected control trees sprayed	needle net assimilation whole-canopy net assimilation	negative needle net carbon balance when pathogen colonization >25% of stomata reduced by 85%	<i>Manter et al.</i> [2003]
parasite 20	dwarf mistletoe (<i>Arceuthobium</i> spp.)	western hemlock	Washington State, US	field measurements	eight trees at one site	ongoing	five severely infested trees	three uninfested trees	maximum photosynthetic rates	in heavily infested trees, photosynthetic rate was half that of uninfested trees	<i>Meinzer et al.</i> [2004]

^aSee text for explanation of abbreviations.

^bStudy identifier used in Figure 2.

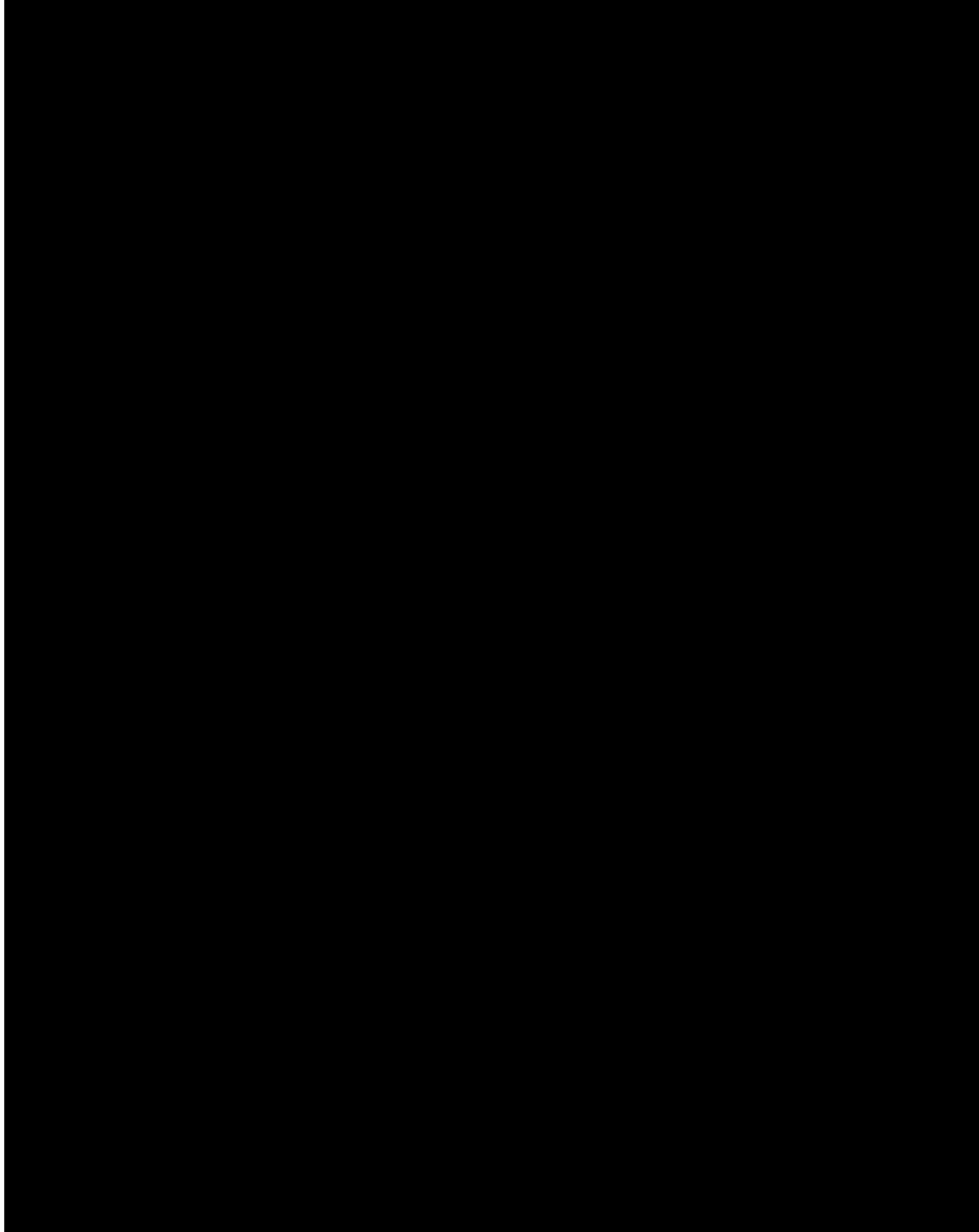


Figure 1. Area affected by major insect species from US and Canadian aerial survey databases. Example species chosen to illustrate variability among species, through time, and between regions. “Affected area” includes live and dead trees. Note that impact on carbon cycle varies across species depending on whether insect is a defoliator (a, b, c, d), which may or may not kill trees, or tree-killing bark beetles (e, f).

Figure 2. Conceptual diagram showing impacts of insect and pathogen outbreaks on carbon budgets. Numbers outside of boxes indicate studies in Tables 3 and 4 that provide evidence. Studies that provide evidence counter to that indicated in diagram noted in bold underlined text (two cases).