Mixedwood management positively affects forest health during insect infestations in eastern North America[1]

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Abstract: Mixedwood stands are composed of hardwoods and softwoods, with neither comprising greater than 75%–80% of basal area or aboveground biomass. By conferring associational resistance and greater resilience to forests when stressed or disturbed, the more diverse composition of mixedwood stands contributes to forest health. We analyzed three examples where mixedwood stands are more resistant to insect infestations in eastern North America. In balsam fir (*Abies balsamea* L. Mill.) and spruce (*Picea* spp.) forests, susceptibility and vulnerability to spruce budworm infestations is reduced with increasing hardwood density. In mid-Atlantic oak-dominated forests, oak mortality following gypsy moth infestations was much greater in oak-dominated forests than in oak–pine mixedwoods, while pine mortality during southern pine beetle infestations was greater in pine-dominated forests than in oak–pine mixedwoods. Overall, mixedwood stands have greater resistance to infestations of defoliators and bark beetles and recover more rapidly from disturbances, reducing economic losses associated with tree mortality and mitigating short-term impacts to ecosystem functioning resulting from insect damage, especially carbon sequestration. Finally, we discuss challenges and opportunities for mixedwood management to minimize insect damage. Management strategies that incorporate mixedwood stands may provide better continuity in supply of forest products and ecosystem services in the face of projected increases in insect infestations associated with changing climate.

Key words: insect outbreaks, insect epidemics, associational resistance, silviculture, defoliation, tree mortality.

Résumé : Les peuplements mixtes sont composés de feuillus et de résineux, ni l'un ni l'autre ne pouvant constituer plus de 75–80 % de la surface terrière ou de la biomasse aérienne. En conférant une résistance d'association et une plus grande résilience aux forêts lorsqu'elles subissent un stress ou une perturbation, la composition plus diversifiée des peuplements mixtes contribuent à la santé de la forêt. Nous avons analysé trois exemples où des peuplements mixtes sont plus résistants aux infestations d'insectes dans l'est de l'Amérique du Nord. Dans les forêts de sapin baumier (*Abies balsamea* L. Mill.) et d'épicéa (*Picea* spp.), la sensibilité et la vulnérabilité aux infestations de la tordeuse des bourgeons de l'épinette diminuent avec l'augmentation de la densité des feuillus. Dans les forêts du centre du littoral atlantique dominées par le chêne, la mortalité du chêne due aux infestations de la spongieuse était beaucoup plus élevée dans les forêts dominées par le chêne que dans les forêts mixtes de chêne et de pin, tandis que la mortalité du pin lors des infestations du dendroctone méridional du pin était plus élevée dans les forêts dominées par le pin que dans les forêts mixtes de chêne et de pin. Dans l'ensemble, les peuplements mixtes ont une plus grande résistance aux infestations d'insectes défoliateurs et de scolytes et récupèrent plus rapidement après une perturbation, ce qui réduit les pertes économiques associées à la mortalité des arbres et atténue les impacts à court terme des dommages causés par les insectes sur le fonctionnement de l'écosystème et plus particulièrement sur la séquestration du carbone. Finalement, nous abordons dans la discussion les défis et opportunités concernant l'aménagement de la forêt mixte dans le but de minimiser les dommages causés par les insectes. Les stratégies d'aménagement qui incluent les peuplements mixtes peuvent assurer une meilleure continuité de l'approvisionnement en produits forestiers et services de l'écosystème face à l'augmentation prévue des infestations d'insectes associées au changement climatique. [Traduit par la Rédaction]

Mots-clés : infestations d'insectes, épidémies d'insectes, résistance d'association, sylviculture, défoliation, mortalité des arbres.

Introduction

Forests composed of a diversity of tree species have a greater range of shade tolerances, growth rates, longevities, phenology, and crown and root structures than pure species stands (Kabrick et al. 2017). Such mixtures diversify ecological niches and accommodate tree species with different ecological requirements through complementary resource use (Coates and Burton 1997; Kneeshaw and Prévost 2007).

Further, more diverse forests have been observed to exhibit reduced susceptibility to insect infestations and pathogens compared with those dominated by a single species (Jactel and Brockerhoff 2007; Jactel et al. 2017; Zhang et al. 2018; Fig. 1). Based on a worldwide meta-analysis of 119 studies that compared herbivory in single-species and mixed forests, Jactel and Brockerhoff (2007) concluded that herbivory was significantly reduced in more diverse forests, but this varied

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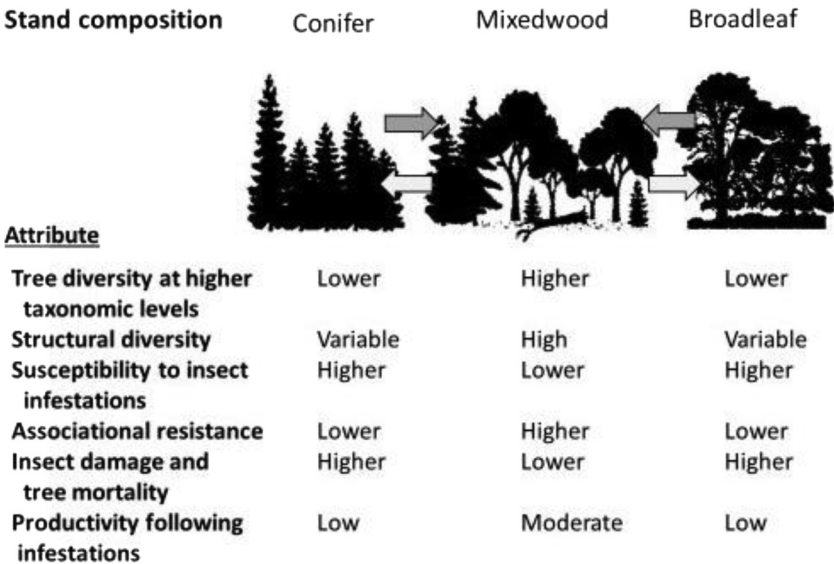**K.L. Clark.** USDA Forest Service, Northern Research Station, Silas Little Experimental Forest, 501 Four Mile Road, New Lisbon, NJ 08064, USA.
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Fig. 1. Composition and attributes of conifer-dominated, mixedwood, and broadleaf-dominated stands. Mixedwood stands have greater diversity at higher taxonomic levels (e.g., family and above) that is more evenly distributed across co-dominant species, although not necessarily a greater number of species. Mixedwood stands typically have greater structural diversity than conifer- or broadleaf-dominated stands. Greater diversity at higher taxonomic levels confers reduced susceptibility to insect infestations, primarily through greater associational resistance. Depending on the insect, damage and tree mortality are reduced compared with conifer- or broadleaf-dominated stands. Successional changes in species composition favors either conifer or broadleaf dominance in the absence of major disturbances, depending on forest type (indicated by the light arrows). In contrast, insect infestations and differential tree mortality can result in the formation of mixed composition stands (indicated by the darker arrows).

Stand composition	Conifer	Mixedwood	Broadleaf
Attribute			
Tree diversity at higher taxonomic levels	Lower	Higher	Lower
Structural diversity	Variable	High	Variable
Susceptibility to insect infestations	Higher	Lower	Higher
Associational resistance	Lower	Higher	Lower
Insect damage and tree mortality	Higher	Lower	Higher
Productivity following infestations	Low	Moderate	Low

with the host specificity of insects. Herbivory by oligophagous species (those that consume plants of closely related genera or a single taxonomic family) was nearly always reduced in diverse forests, but the response of polyphagous species that consume a wide variety of plants was weaker (Jactel and Brockerhoff 2007). The species composition of tree mixtures was more important than species richness per se, and effects of diversity on herbivory were greater when mixed forests comprised taxonomically more distant tree species or when the proportion of non-host trees exceeded that of host trees (Jactel and Brockerhoff 2007; Fig. 1).

Diverse species composition of forests may decrease the likelihood of detection by, and (or) vulnerability to, herbivores, termed associational resistance (Barbosa et al. 2009). Specific mechanisms involved in greater associational resistance to insect pests include: (*i*) host dilution due to intermingling with non-host species in diverse stands, affecting how insects perceive the overall quality of a stand and lowering their probability of finding and feeding on host trees; (*ii*) lower visual or chemical apparency of individual host trees within a stand when their frequency is lower relative to non-host trees; and (*iii*) greater diversity of parasitoids or predators associated with increased diversity of predator habitats. In contrast, increased detection by and (or) vulnerability to herbivores in diverse stands is an example of associational susceptibility. Associational resistance is more likely with insects, while associational susceptibility is more likely with mammals (Barbosa et al. 2009).

One commonly used category of diverse forests is mixed hardwood–softwood (broadleaved–conifer) forests or "mixedwoods", which are composed of stands where neither group comprises greater than 75% to 80% of basal area or aboveground biomass (e.g., Kabrick et al. 2017). There is considerable interest in mixedwood silviculture and management to diversify timber products and ecosystem services and maintain diverse forest landscapes (Kenefic et al. 2021; Vickers et al. 2021). Mixedwoods comprise a large portion of North American forests, with 111 million hectares of mixedwood forest (defined as mixed coniferous and broadleaf trees, each between 25% and 75%) representing 17% of

the total (North American Forest Database 2020; Vickers et al. 2021). Some mixedwood species combinations are challenging to manage (Smith 1986; Kern et al. 2021), and historically, many have been managed for softwood species and products (e.g., Westveld 1930; Lieffers and Beck 1994; Etheridge et al. 2006; Kenefic et al. 2021). Mixedwood stands may be multistoried, especially in early stand development stages, or have only a single canopy layer, and structure often changes over time from an early dominant hardwood overstorey and a softwood understory that gradually grows into the main canopy and eventually overtops the hardwood trees (Comeau 1996). This pattern contrasts with pine-dominated forests in the mid-Atlantic and mid-western regions, which are maintained by disturbance (primarily fire), and oaks and other hardwoods tend to dominate through time (Little 1998; Nowacki and Abrams 2008; Kenefic et al. 2021).

Paralleling observations in forests with high diversity, there is strong evidence that mixedwood management has benefits in reducing insect herbivory and associated impacts compared with pure species stands, with either the softwood or hardwood component likely to experience less damage or mortality depending on the species of insect (Fig. 1). These benefits often exceed the effect expected by just replacing host with non-host species (Jactel and Brockerhoff 2007; Campbell et al. 2008; Jactel et al. 2017; Zhang et al. 2018). In addition, mixedwoods can potentially provide greater timber volume or biomass and more diverse habitats and be more resistant or resilient to pathogens and other disturbances than pure stands (Cavard et al. 2011; Kabrick et al. 2017). Mixedwoods are also thought to be more compatible with projected future climates; all five mixedwood stand types examined by Kabrick et al. (2017) appeared to be better adapted to a changing climate than pure softwood stands.

Insect damage that results in tree growth reduction or mortality has multiple effects on community dynamics and ecosystem functioning, including succession, competition, productivity, nutrient cycling, energy flow, and carbon sequestration (Fig. 1). Most insects are specialists that target either individual (or multiple)

Table 1. Gradient of susceptibility of dominant tree species in the northeast to spruce budworm, gypsy moth, and southern pine beetle.

Susceptibility	Spruce budworm	Gypsy moth	Southern pine beetle
Highest	Balsam fir	Red, white, black, and scarlet oaks	Loblolly pine
	White spruce	Chestnut oak	Pitch pine
	Red spruce	Sweetgum	Shortleaf pine
	Black spruce		Virginia pine
	Eastern larch	Cottonwood and Aspen	White pine
	Eastern hemlock	Birch and Alder	(Jack pine)*
		Sugar maple	
		White pine	
		Eastern hemlock	
		Red maple	
Lowest		Ash and Tulip poplar	
Nonsusceptible	Hardwoods	Most softwoods	Hardwoods

*Susceptibility to southern pine beetle not well known.

conifer or deciduous species. Therefore, the most basic difference between mixedwood (or any diverse species stand) and pure stands is that a portion is not susceptible to damage. The non-susceptible species may undergo increased growth and reduced competition in response to the insect outbreak of host species (e.g., increased growth of hardwood species in mixed hardwood–fir stands during spruce budworm outbreaks; Hennigar et al. 2007b) A variety of short-term impacts of insect infestations on ecosystem functioning are relatively well characterized in some regions (e.g., in mid-Atlantic; Clark et al. 2010, 2014, 2018; Amiro et al. 2010; Deel et al. 2012; Renninger et al. 2014). In addition, a number of simulation models have captured the overall dynamics of carbon, hydrologic, and nutrient cycling associated with these disturbances (Medvigy et al. 2012; Kretchun et al. 2014; Xu et al. 2017). In summary, infestations of defoliators and bark beetles initially reduce leaf area of infested stands as a function of defoliation intensity or tree and sapling mortality. This causes an immediate decline in photosynthetic capacity, which decreases net ecosystem productivity (NEP) and C sequestration but enhances litterfall of nutrient-rich litter and, in the case of defoliators, frass. Similarly, reduced leaf area results in lower rates of evapotranspiration (Et; Clark et al. 2012). Compensatory photosynthesis by the remaining foliage, which is typically exposed to higher light levels, and the rapid cycling of nutrients from nutrient-rich frass and (or) litter facilitates resprouting of new foliage (Curtis and Gough 2018; Hornslein et al. 2019). As a result, gross ecosystem productivity (GEP), Et, and ecosystem water use efficiency (WUE$_e$), defined as the amount of CO_2 assimilated per unit of water transpired, often recover rapidly following insect damage (Clark et al. 2014; Guerrieri et al. 2019). In contrast, tree and sapling mortality resulting from repeated defoliation or bark beetle infestations increases standing dead and coarse woody material, resulting in increased heterotrophic respiration and a long-term depression of NEP (Renninger et al. 2014; Xu et al. 2017; Clark et al. 2018; Fig. 1). Defoliation or reduced leaf area increases light penetration into the understory, which promotes growth of advance regeneration and non-host species (e.g., Nie et al. 2019) and may make the stand more susceptible to fire (e.g., Stocks 1987) or windthrow (Taylor and MacLean 2009).

In this paper, we review the role of mixedwoods in three important insect–forest systems in eastern North America. We focus on effects on defoliation or damage, growth reduction, tree mortality, and ecosystem functioning, primarily patterns of carbon sequestration during and following insect infestations. We describe the evidence for, and mechanisms involved in, mixedwood resistance and resilience to insect damage in spruce budworm (*Choristoneura fumiferana* Clem.) in balsam fir (*Abies balsamea* L. Mill.) and spruce (*Picea* spp.) forests, gypsy moth (*Lymantria dispar* L.) in oak (*Quercus* spp.) and pine (*Pinus* spp.) forests, and southern pine beetle

(*Dendroctonus frontalis* Zimmermann) in pine, oak, and other hardwood forests.

Effects of mixedwoods on insect damage in three North American ecosystems

Spruce budworm and balsam fir defoliation, growth reduction, and mortality

Spruce budworm causes the most damaging outbreaks in eastern North America, periodically occurring about every 30–40 years over millions of hectares of balsam fir and spruce forests. When budworm larvae defoliate a tree, they remove a portion of the photosynthetic factory as well as sites where chemicals such as growth hormones are produced, and this affects many vital functions (MacLean 1985). Repeated annual defoliations, which typically can last for 5–10 years during an outbreak, cause reduction of wood production, tree mortality, and decreased stand yield (e.g., Kulman 1971). Tree mortality usually begins after about 4 years of defoliation for balsam fir and 6–7 years for spruce (MacLean 1980). This is not new information; data on losses caused by spruce budworm were published nearly 100 years ago by Swaine and Craighead (1924) and Craighead (1925). There has been continued interest and research to the present about spruce budworm damage because of the large extent of outbreaks (covering 52 million hectares of Canada in 1975; MacLean 2016) and the severe tree mortality (e.g., MacLean 1980) and timber supply and economic losses (e.g., Chang et al. 2012; Hennigar et al. 2013).

Changing stand composition by maintaining or increasing hardwoods in balsam fir stands has long been proposed as a silvicultural technique to reduce susceptibility (probability of being attacked) and vulnerability (probability of growth reduction or mortality once attacked) to spruce budworm (Westveld 1946; Blum and MacLean 1984, 1985; Carlson and Wulf 1989; Hudak 1991). Defoliation level (susceptibility) declines in the order balsam fir > white spruce (*Picea glauca* (Moench) Voss) > red spruce (*Picea rubens* Sarg.) > black spruce (*Picea mariana* (Mill.) B.S.P.) (Hennigar et al. 2008; Table 1). Thus, silvicultural recommendations to reduce spruce budworm damage have largely been to reduce balsam fir at the stand and landscape levels through spruce plantation establishment or pre-commercial thinning that favors spruce species over balsam fir (Blum and MacLean 1984, 1985). In addition, Croome (1970) and van Raalte (1972) suggested that 30%–60% of stand composition in non-host species was needed for a major reduction in susceptibility. Balsam fir mortality caused by spruce budworm defoliation declined from >80% to <50% as the percentage of hardwoods increased from 0% to 30% (Turner 1952). Mixedwood stands with at least 30% hardwoods sustained budworm-caused mortality that was 30% less than in pure fir stands (MacLean 1980).

Hypotheses proposed to explain the mechanisms resulting in lower defoliation and impacts with increased hardwood content include (*i*) dispersal losses of first- and second-instar spruce budworm larvae during dispersal to other hosts (Kemp and Simmons 1978; Zhang et al. 2020), both within stands and between stands if the stand edge to area ratio is high (Roland 1993; Kouki et al. 1997); (*ii*) a more abundant and diverse complex of budworm natural enemies, including higher tachinid parasitism of larvae and ichneumonid parasitism of pupae in fir stands isolated by hardwood forests (Cappuccino et al. 1998) and higher hymenopteran parasitism of budworm eggs in in mixed fir–hardwood than in balsam fir stands (Quayle et al. 2003); and (*iii*) higher larval predation by a potentially more diverse community of birds at forest edges and in mixedwoods (Crawford and Jennings 1989; Drapeau et al. 2000). Quayle et al. (2003) specifically concluded that parasitism was particularly important in mixedwood stands.

Mixedwood stand composition has been shown to reduce defoliation levels during spruce budworm outbreaks. Defoliation in 25 mixed balsam fir–hardwood stands, over 5 years near the end of a spruce budworm outbreak in New Brunswick, Canada, was significantly negatively related to hardwood content (Su et al. 1996). Ten balsam fir stands with <40% hardwoods sustained 58%–71% defoliation, whereas five stands with >80% hardwoods had only 12%–15% defoliation (Su et al. 1996). Zhang et al. (2018) also tested the influence of stand composition on defoliation, but during the first 5 years of a spruce budworm outbreak in Quebec, Canada. Defoliation of fir in 27 balsam fir–hardwood plots representing softwood, mixedwood, and hardwood compositions was significantly lower as hardwood content increased. Percent hardwood content and average defoliation in softwood plots (an indicator of overall outbreak severity) were the most important variables in a Random Forests model of annual defoliation per plot (Zhang et al. 2018). Mean defoliation differed significantly among stand types, with softwood > mixedwood > hardwood in 2 years and with softwood > hardwood in all 5 years tested. Zhang et al. (2020) determined that increasing hardwood content increased second-instar budworm larvae (L2) dispersal losses, but in their case, stand type did not significantly affect parasitism rates. L2 dispersal loss was less in softwood than in mixedwood or hardwood stand types based on measurements on ground traps and less in softwood and mixedwood than in hardwood stands based on sampling budworm larvae on regeneration (Zhang et al. 2020).

Hardwood content of surrounding forest landscapes also influences spruce budworm damage. Campbell et al. (2008) evaluated factors influencing radial growth reductions during a budworm outbreak and found that hardwood content of surrounding (within 1 km) landscapes was a significant factor explaining variance in budworm-caused growth reductions. For example, in a peak outbreak year, mean growth reduction was ~40% in stands with <50% surrounding hardwood content versus ~20% with >50% surrounding hardwoods (Campbell et al. 2008).

Associational susceptibility has also been observed in some species mixtures during spruce budworm infestations, resulting in defoliation and subsequent growth reduction and mortality of non-preferred species. For example, the presence of balsam fir in a stand can increase defoliation of the lower susceptibility black spruce (Bognounou et al. 2017) and eastern hemlock (*Tsuga canadensis* (L.) Carrière), although usually considered non-host species for spruce budworm.

If the management objective is primarily to produce softwood products, replacing balsam fir with hardwoods also reduces the fir softwood volume, so what is the best hardwood–softwood level? It depends on outbreak severity. Needham et al. (1999) analyzed trade-offs between reduced defoliation and mortality versus the amount of balsam fir volume reduction from allocating growing space to hardwoods. Optimum hardwood levels varied with the severity of spruce budworm attack: below a 45% defoliation level (5-year average), the reduction of fir volume replaced by hardwoods exceeded

Fig. 2. Merchantable volume of balsam fir and hardwood trees before infestation ("Pre") and a decade following infestations ("Post") by spruce budworm in balsam fir dominated (BF), balsam fir –hardwood mixedwood (MW), and hardwood-dominated (HW) stands. Data were modified from Needham et al. (1999), where BF included 0%–20% hardwood classes, MW included 30%–70% hardwoods, and HW included 80%–100% hardwoods.
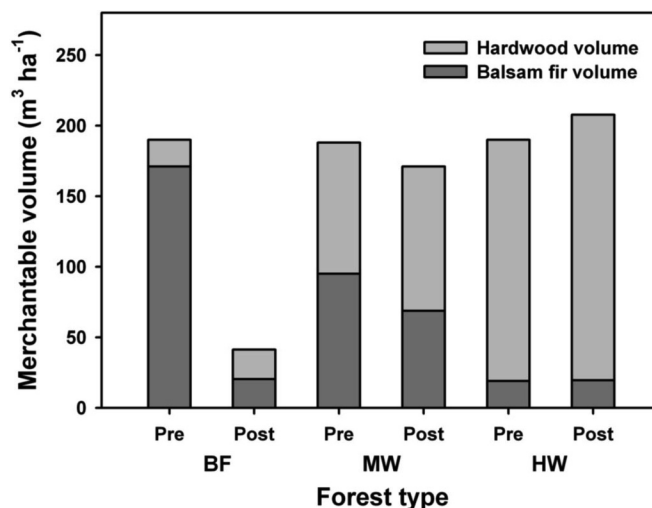
the volume protected, but with defoliation > 75%, maximum softwood production was achieved with hardwood content comprising 50% of stand volume (Needham et al. 1999). This is depicted for generalized balsam fir, mixedwood, and hardwood forest classes in Fig. 2. On average, the spruce budworm infestation reduced balsam fir merchantable volume by 88% in mature balsam fir stands but only by 28% in mixedwood stands, and balsam fir volume increased slightly during the outbreak in hardwood stands (Fig. 2).

Spruce budworm outbreaks influence stand species composition. In mature balsam fir stands, species composition 30 years following a budworm outbreak was closely related to pre-disturbance species composition, but in immature fir stands, hardwood composition increased by up to 27% (Spence and MacLean 2012). Seedling density of advanced balsam fir regeneration decreased over a 10-year outbreak period, but average height of surviving seedlings increased by up to five times as the canopy cover decreased with tree mortality (Spence and MacLean 2012).

Spruce budworm outbreaks and mixedwood content also have major effects on forest carbon. Hennigar and MacLean (2010) calculated potential spruce budworm outbreak and management strategy (salvage, biological insecticide application) effects on forest and wood product carbon (C) over 50 years for a 210 000 ha intensively managed forest in New Brunswick, Canada. Harvest volume, forest C storage, and wood product C storage were projected to be reduced, compared with a no-outbreak scenario, by 1.34 million m³, 1.48 million tonnes C, and 0.26 million tonnes C, respectively. Modelling analyses indicated that use of salvage and harvest replanning plus a biological insecticide applied aerially to 40% of susceptible forest area were projected to reduce future spruce budworm impacts on harvest losses by 73%, forest C losses by 41%, and wood product C losses by 56% (Hennigar and MacLean 2010). Hardwood volume increases 15 years after the outbreak resulting from reduced stand competition from mortality of spruce–fir averaged one-third to one-half in immature mixedwood stands, which offset some of the C impacts. This effect was augmented by lower specific gravity of spruce (~0.37) and fir (0.33) compared with hardwood species (e.g., poplar, 0.35; white birch, 0.48; red maple, 0.49; sugar maple,~0.55) (Green et al. 1999). As a result, C in living biomass 15 years after the outbreak was reduced by 8%,

substantially less than the 24% total volume reduction. Dymond et al. (2010) also showed that a spruce budworm outbreak would significantly affect the C sink or source status of a large landscape (106 000 km^2 of forest in eastern Quebec). Projections with a model of ecosystem C showed that mortality caused by spruce budworm decreased stand-level merchantable C stocks by up to 90% and changed the landscape from a sink to a source due to reduced net primary production (Dymond et al. 2010). The ecosystem C stock was reduced on average by 2 Tg C·year^{-1} for the simulated area (Dymond et al. 2010); however, Dymond et al. (2010) did not explicitly model competitive release of hardwoods following severe defoliation or reduced defoliation levels of host species associated with hardwoods.

Gypsy moth and oak defoliation, growth reduction, and mortality

European gypsy moth is one of the more destructive forest insects in eastern North America, defoliating an average of 400 000 ha of forest per year, with a maximum of 5 million hectares in 1981 (McManus et al. 1992). Since their introduction in Massachusetts in 1869, the European gypsy moth has spread throughout the Northeast and mid-Atlantic regions of the United States (US) to portions of the Midwest US and to southeastern Canada (USDA Forest Service 2020). The gypsy moth primarily defoliates oaks and other hardwood species, and although severe infestations can result in complete defoliation of both hardwood and softwood species, repeated defoliation over consecutive growing seasons typically results in significant mortality of vulnerable hardwood trees and saplings (Mosher 1915; Brown et al. 1988; Davidson et al. 1999; Morin and Liebhold 2016; Table 1). Gypsy moth damage has reduced oak productivity and regeneration across much of the range where they overlap, contributing to regional oak decline (Morin and Liebhold 2016; Fei et al. 2019). Tree mortality has decreased the supply of high-quality hardwood sawlogs and resulted in increased density of less commercially important species such as American beech (*Fagus grandifolia* Ehrh.) and red maple (*Acer rubrum* L.) (www.fia.fed.us). There is continued interest in control and mitigation of gypsy moth damage, because the gypsy moth has impacted less than 25% of their potential range in North America, and all vulnerable hardwood species are potentially at risk.

Stand composition alters susceptibility and mortality from gypsy moth (Mosher 1915; Clement and Munro 1917; Brown et al. 1988). Oak-dominated stands in oak–hickory and northern hardwood forests are most vulnerable, with repeated defoliation over consecutive growing seasons resulting in progressively greater levels of reduced growth and mortality (Davidson et al. 1999; Fei et al. 2019). Stands consisting of mixtures of softwoods and hardwoods demonstrate both associational resistance and associational susceptibility to gypsy moth infestations, depending on defoliation intensity and stand species composition (e.g., Jactel et al. 2017). For example, in a recent severe gypsy moth infestation on the mid-Atlantic coastal plain, approximately 40% of oak trees died following repeated defoliation over 2 to 3 years in oak-dominated stands, while oak mortality was much lower in mixedwood oak – pitch pine stands and minimal in pitch pine dominated stands where post oak (*Quercus stellata* Wangenh.) and white oak (*Quercus alba* L.) represented <10% of basal area (Fig. 3a; Clark et al. 2010, 2018). Further south, loblolly pine – hardwood stands experienced lower mortality from gypsy moth than oak-dominated stands, with greater mortality occurring in loblolly pine – oak stands than in loblolly pine – sweetgum (*Liquidamber styraciflua* L.) stands, but mature loblolly pine mortality was low (Eisenbies et al. 2007).

Associational susceptibility of softwood trees and saplings to gypsy moth infestations in mixedwood stands depends on the softwood species and canopy position, as well as the density of vulnerable hardwoods and intensity of defoliation. For example, >80% defoliation of eastern white pine (*Pinus strobus* L.) in stands containing northern red oak (*Quercus rubra* L.) significantly

increased mortality of intermediate and suppressed pines (Brown et al. 1988; Gottschalk and Twery 1989), while mortality of pitch (*Pinus rigida* Mill.) and shortleaf (*Pinus echinata* Mill.) pine trees and saplings was minimal in stands containing black oak (*Quercus velutina* Lam.) (Campbell and Garlo 1982; Clark et al. 2018). Eastern hemlock in red oak – softwood stands were highly vulnerable to defoliation by gypsy moth, with highest mortality occurring in intermediate and suppressed trees and understory saplings (Stephens 1988). Hennigar et al. (2007a) observed that gypsy moth infestations resulted in unexpectedly large growth reductions and mortality of balsam fir, white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.) in stands containing northern red oak in central New Brunswick, Canada. Collectively, these results indicate that mixedwood stands often have lower tree mortality following gypsy moth infestations, but interactions between defoliation intensity and frequency and stand species composition are important in determining patterns of defoliation, growth reduction, and mortality.

Silvicultural treatments to enhance resistance to the gypsy moth have been proposed since the early 1900s, but few long-term experiments testing the increased resistance of mixedwood vs. hardwood-dominated stands have been conducted (Clement and Munro 1917; Muzika 2017). Initial prescriptions sought to shift the emphasis from eradication to mitigation by reducing the density of vulnerable species (Behre 1939). Pre-infestation crown condition is a strong indicator of mortality of vulnerable species following gypsy moth infestations, but not necessarily crown class or tree size, thus mortality is difficult to predict a priori in the field for all but the most stressed trees. Thinning treatments alone have been inconclusive, with some studies demonstrating reduced mortality and greater stem increment growth following gypsy moth infestations (Muzika et al. 1998) but not others (Fajvan et al. 2008). Prescriptions for sanitation thinning and pre-salvage thinning have been used to remove vulnerable species and increase stand vigor, with thinning of vulnerable species to <50% of stand basal area described as beneficial and thinning to <20% of stand basal area described as best for reducing mortality of commercially important oaks, although these levels may be difficult and expensive to achieve (Gottschalk and Twery 1989; Gottschalk 1993).

In some cases, uneven-aged forests have greater resistance to insect infestations and other disturbances than even-aged forests (Jactel et al. 2017); however, many of the forests in the mid-Atlantic and northeastern US impacted by gypsy moth infestations are intermediate-aged, following recovery from extensive logging, agricultural use, and abandonment and, in some areas, severe wildfires, and thus do not encompass the full range of age classes (Pan et al. 2011; Duveneck et al. 2017; Stambaugh et al. 2018). As these forests age, simulating natural successional processes (or delaying them) through silvicultural management to create more resistant and resilient mixedwood forests is possible (Webster et al. 2018; Willis et al. 2019; Kenefic et al. 2021). Treatments combining multi-aged mixedwood management in the prescription could be particularly successful (Castagneyrol et al. 2020). In some mid-Atlantic forests, insect infestations are doing just that; for example, by promoting the regeneration and growth of pine seedlings and saplings in previously oak-dominated stands, gypsy moth infestations and subsequent mortality may be driving the formation and persistence of uneven-aged mixedwood stands. Overstory mortality in oak-dominated stands releases pine seedlings and saplings in the understory, and a decade after gypsy moth infestation, pine trees and saplings increased from 25% to 39% of basal area, with a 10-fold increase in pine saplings (Fig. 3a). Relative basal area has converged with that characterizing oak–pine mixedwood stands (Fig. 4, left arrow). As these uneven-aged mixedwood stands recover, they are likely to be more resistant to damage from future gypsy moth infestations, much like the mixedwood stand in Fig. 3a. Overall, designing and implementing disturbance-based management strategies that

Fig. 3. (*a*) Basal area of oak and pine trees and saplings before infestation (2004; "Pre") and a decade following infestations by gypsy moth (2018; "Post") in oak-dominated, oak–pine mixedwood, and pine-dominated stands. Dominant canopy trees were similar in age. Pre-infestation census data are from Clark et al. (2010, 2018); post-infestation from same sets of plots, unpublished data. (*b*) Basal area of pine, oak, and other hardwood trees and saplings before and following infestation of southern pine beetle in pine-dominated stands (from Clark et al. 2017, 2020).
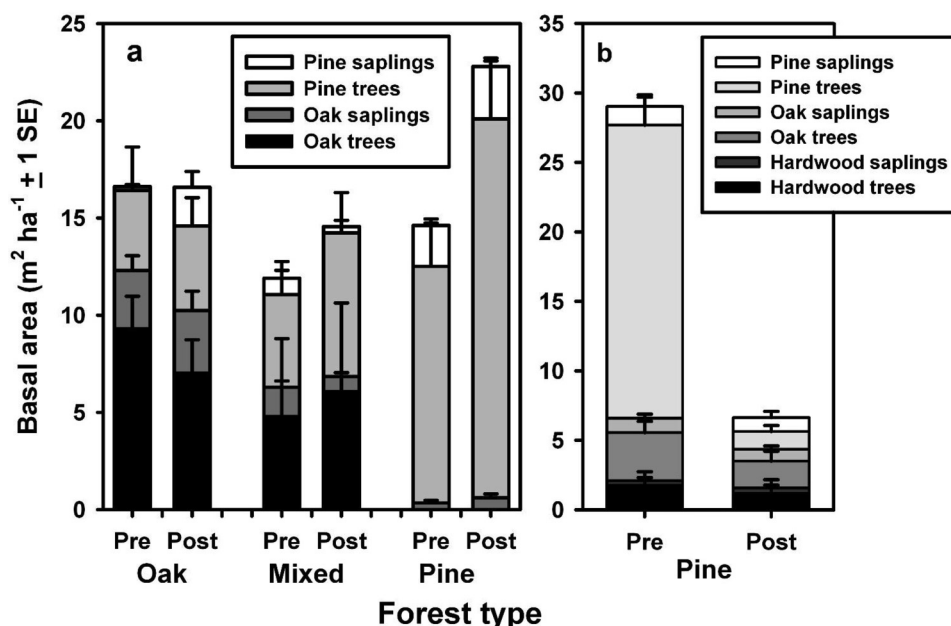

Fig. 4. Relative basal area of an oak-dominated stand before ("Pre") and following ("Post") severe gypsy moth defoliation, an oak–pine mixedwood stand, and pitch pine stands before ("Pre") and following ("Post") southern pine beetle infestation in the Pinelands National Reserve of New Jersey. Arrows indicate the directional changes in relative basal area caused by insect damage; the arrow on the left indicates gypsy moth damage and the arrow on the right indicates southern pine beetle damage. Adapted from census data in Clark et al. (2017, 2018, 2020).
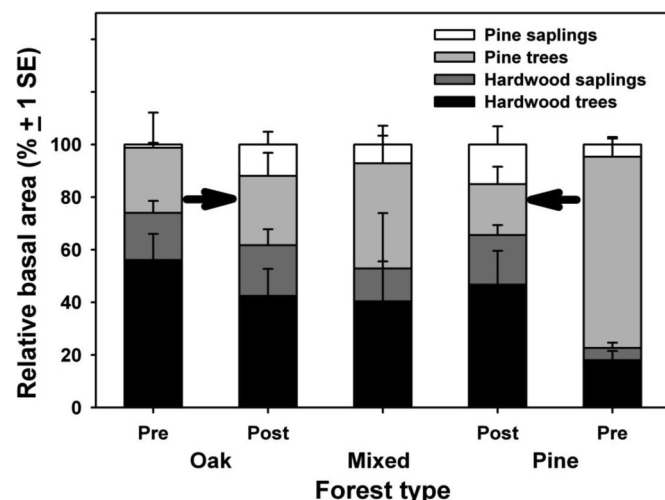
mimic similar responses in other forest systems could help to mitigate the impacts of future insect infestations (Webster et al. 2018; Puettmann and Messier 2020).

Gypsy moth infestations have reduced forest productivity and carbon sequestration by impacted forests throughout the northeastern and mid-Atlantic regions of the US, with impacts generally proportional to defoliation severity and the density of vulnerable species

(Clark et al. 2010; Kautz et al. 2017; Xu et al. 2017; Kosiba et al. 2018). US Forest Service Forest Inventory and Analysis (FIA) data indicate that net primary productivity (NPP) in the dominant oak–hickory, mixedwood oak–pine, and pine-dominated forest types in the absence of gypsy moth infestations are similar, and net ecosystem productivity (NEP) ranges between 1.7 and 2.1, 1.2 and 1.7, and 1.0 and 1.6 tonnes (t) $C \cdot ha^{-1} \cdot year^{-1}$, respectively (https://www.fia.fs.fed.us). These are similar to pre-infestation annual NEP values of 1.8, 1.4, and 1.7 t $C \cdot ha^{-1} \cdot year^{-1}$ for oak-dominated, mixedwood, and pine-dominated stands in the Pinelands National Reserve of New Jersey (Table 2; Clark et al. 2010, 2018), about 20% of which were heavily to severely defoliated (New Jersey Department of Agriculture 2021; USDA Forest Service 2005–2016), reducing NEP to −2.5, −0.2 and 0.4 t $C \cdot ha^{-1} \cdot year^{-1}$, respectively (Table 2). Clark et al. (2010) estimated that annual landscape-scale C uptake was reduced by approximately 40%. Mortality in oak-dominated stands reduced oak tree and sapling basal area compared with peak pre-defoliation values, and in the following years, there was no net increase in basal area or aboveground biomass (Fig. 3*a*). NEP has been depressed for a decade, averaging only 0.4 t $C \cdot year^{-1}$, 22% of pre-defoliation values (Clark et al. 2018), and enhanced ecosystem respiration can depress NEP for up to two decades as standing dead and coarse woody material decompose (Renninger et al. 2014).

In contrast, in mixedwood oak–pine stands, oak tree and sapling mortality was minor following infestations (Fig. 3*a*). Basal area of trees and saplings had increased by 22% by 2018 compared with 2004, with increases in both pine and oak tree basal area resulting from ingrowth and sapling recruitment (Fig. 3*a*). Mixedwood oak–pine stands that incurred lower amounts of mortality and coarse woody material recruitment exhibited lower ecosystem respiration rates and a more rapid recovery in NEP following infestations (Kretchun et al. 2014). In pine-dominated stands, oak mortality was minimal following gypsy moth infestations. While defoliation of oaks and shrubs reduced annual NEP to only 23% of values in undisturbed years, ingrowth and sapling recruitment increased basal area by 56% between 2004 and 2018 (Table 2; Fig. 3*a*), and NEP was similar to pre-infestation levels within 2 years

Table 2. Net ecosystem production (NEP), gross ecosystem production (GEP), and evapotranspiration (Et) before and during severe defoliation by gypsy moth in the New Jersey Pinelands National Reserve.

Forest type	NEP (g C·m^{-2}·year^{-1})		GEP (g C·m^{-2}·year^{-1})		Et (mm·year^{-1})	
	Before	During	Before	During	Before	During
Oak	183	−246	1503	726	637	442
Mixedwood	137	−20	1205	992	607	419
Pine	173	40	1633	1402	757	593

Note: The oak stand was dominated by chestnut (*Quercus prinus*), white (*Q. alba*), black (*Q. velutina*), and scarlet (*Q. coccinea*) oaks and shortleaf (*Pinus echinata*) and pitch (*P. rigida*) pines; the mixedwood stand was co-dominated by chestnut and white oaks and pitch pine; and the pine stand was dominated by pitch pine and white and blackjack (*Quercus stellata*) oaks. Adapted from Clark et al. (2010, 2014, 2018).

(Clark et al. 2018). Overall, growth and NEP were greater in mixedwood stands during gypsy moth defoliation and recovered to pre-infestation levels rapidly compared with severely infested oak-dominated stands.

Southern pine beetle and pine mortality

Southern pine beetle is native to the southeastern US, south through Mexico, and west to Texas, but recently its range has extended northward on the Atlantic coastal plain into New Jersey and Long Island, New York, and it has been detected further north in forests dominated by pitch pine (*Pinus rigida*) (Weed et al. 2013; Clark et al. 2017; Dodds et al. 2018; Heuss et al. 2019). It has also expanded westward into southern Missouri, Illinois, and Ohio. Southern pine beetle infests primarily hard pines (Nowak et al. 2015; Dodds et al. 2018). On the Atlantic coastal plain, loblolly (*Pinus taeda* L.), shortleaf (*Pinus echinata*), pitch, and Virginia (*Pinus virginiana* Mill.) pines are susceptible (Table 1), while white pine susceptibility in northeastern forests is not as well known (Dodds et al. 2018). Further northward expansion into forests composed of red pine (*Pinus resinosa* Aiton) and jack pine (*Pinus banksiana* Lamb.) is projected in the future, following isoclines of increasing winter temperatures with changing climate (Lesk et al. 2017; Dodds et al. 2018). Pitch pine is not a particularly important commercial species in the region, but white pine is, thus further expansion of southern pine beetle into forests of the northeastern US and Canada could impact softwood sawlog and pulpwood products.

Overall stand density and the relative importance of pines are critical factors in the probability of southern pine beetle leading to pine tree and sapling mortality, with basal areas greater than 28 m^2·ha^{-1} considered highly susceptible (Guldin 2011). Stand density (as reflected in basal area) is proportional to turbulence regimes within forest canopies, altering dispersion of aggregation pheromone released by southern pine beetle (Thistle et al. 2004; Edburg et al. 2010). The recent infestations in New Jersey and New York occurred in relatively dense pine-dominated stands that exceeded the target basal area of 18 m^2·ha^{-1} that has been effective in reducing southern pine beetle damage in southern US forests (discussed later). Recent infestations resulted in extensive mortality of pitch, shortleaf, and Virginia pine trees, averaging 94% of pine tree basal area, while pine saplings were infested less frequently, and pine sapling basal area was similar in uninfested and infested areas (Fig. 3*b*; Clark et al. 2017; Aoki et al. 2018). Southern pine beetle infestations (and suppression treatments) had little effect on oak trees and saplings or other hardwoods such as red maple and black gum (*Nyssa sylvatica* Marshall) (Fig. 3*b*). Southern pine beetle rarely impacted pines in oak-dominated stands, and tree mortality was lower in mixedwood stands, a pattern also documented by Heuss et al. (2019) in New York, where mortality averaged 60% of total basal area in stands dominated by pitch pine versus 50% and 35% in unmanaged and managed pine–oak stands, respectively.

Silvicultural treatments to reduce southern pine beetle damage include thinning of dense stands before outbreaks, with a target basal area for southern pines of 18 m^2·ha^{-1} (Guldin 2011). In unmanaged pitch pine stands in New Jersey and New York, thinning to reduce basal area to approximately 18 m^2·ha^{-1} and prescribed fire to reduce understory competition has been recommended (Dodds et al. 2018). Sanitation cutting of infected green trees and salvage cutting of dead trees impacted by southern pine beetle are often used as suppression treatments to isolate an infestation and reduce its spread (Guldin 2011). Much like the long-term effects of gypsy moth in oak-dominated stands, changes in stand composition and structure in previously pine-dominated stands infested by southern pine beetle in southern New Jersey have converged on structural attributes characterizing mixedwood stands. Relative basal area of trees and saplings in untreated pine stands are now similar to that characterizing mixed oak–pine stands (Fig. 4, right arrow). Heuss et al. (2019) reported a similar pattern following southern pine beetle infestations and pine mortality in New York.

Recent infestations of southern pine beetle in the mid-Atlantic region have significant impacts on ecosystem functioning and carbon dynamics of pine-dominated stands (Fig. 3*b*; Heuss et al. 2019; Clark et al. 2020). Projected leaf area and canopy nitrogen content of remaining trees and saplings in infested stands in New Jersey were less than half of pre-infestation values 3 to 5 years following extensive pine mortality (Clark et al. 2017, 2020). Clark et al. (2014, 2018) and others have shown significant positive relationships between leaf area, canopy N content, and GEP, indicating that GEP and NEP will be reduced in the decades following southern pine beetle infestations. Simulations of C dynamics indicated that annual NEP averaged 1.8 t C·ha^{-1}·year^{-1} in uninfested pine-dominated stands compared with −5.2 t C·ha^{-1}·year^{-1} in infested stands and −4.8 t C·ha^{-2}·year^{-1} in infested stands where cut-and-leave suppression treatments had been conducted (Clark et al. 2020). In infested stands, standing dead trees and coarse woody material increased simulated annual ecosystem respiration up to 1.2 times the values for uninfested areas and increased heterotrophic respiration will further depress NEP (Renninger et al. 2014; Clark et al. 2018). Because reduction in GEP and increased ecosystem respiration are largely proportional to pine mortality, net productivity and NEP will recover relatively rapidly in mixedwood stands that experience lower levels of damage and mortality (Heuss et al. 2019; Clark et al. 2020).

Although seasonal differences occur, carbon and hydrologic fluxes indicate that oak–pine mixedwood stands function similarly to oak- and pine-dominated stands when values are integrated over annual time scales (Clark et al. 2010, 2014). Because oaks and other hardwoods experience lower mortality in mixedwood stands following gypsy moth infestations and pitch and shortleaf pine experience lower mortality in mixedwood stands during southern pine beetle infestations (Clark et al. 2018; Heuss et al. 2019), mixedwood stands maintain greater continuity in ecosystem functioning through time. Both decreased loss of leaf area and foliar nutrients in the short term and reduced

production of snags and coarse woody material following mortality in the long term contribute to the maintenance of ecosystem functioning.

Principles, commonalities, and management implications

Disturbance regimes in eastern North American forests over the last two decades have been dominated by insect damage, with impacts resulting from infestations of both native and non-native insects (Lovett et al. 2016; Kautz et al. 2017; Kosiba et al. 2018; Pasquarella et al. 2018; Fei et al. 2019). n previous decades (from 1975 to 2000), the total (summed) area of moderate to severe (30%–100%) defoliation or beetle-killed trees was 709 million hectares, with 64% caused by spruce budworm, 27% by forest tent caterpillar (*Malacosoma disstria* Hübner), 2% by jack pine budworm (*Choristoneura pinus* Freeman), and the remaining 7% caused by 39 other recorded insect species (MacLean 2016). In many cases, mixedwood stands are less vulnerable to insect infestations than forests dominated by a single species or genus, especially for monophagous insects (Jactel and Brockerhoff 2007; Jactel et al. 2017). Where mixedwood forests consist of mixtures of vulnerable and less vulnerable species, associational resistance reduces the severity of infestations and subsequent tree and sapling mortality, although resistance can change as stands age (Castagneyrol et al. 2020). Employing disturbance-based management to modify stand species composition and structural attributes, including simulating or delaying natural successional processes, as well as multi-aged management of mixedwood stands can create more resistant and resilient forests (e.g., Webster et al. 2018; Puettmann and Messier 2020). Such carefully designed silvicultural treatments would provide lower mortality of commercially important species in some forest types (Gottschalk 1993; Guldin 2011; Heuss et al. 2019). Following infestations, lower rates of mortality in mixedwood stands result in more rapid recovery of leaf area and productivity, as well as reduce ecosystem respiration associated with stem decomposition, and a faster recovery to pre-infestation rates of growth and NEP.

In this paper and in most other related literature, the approach to assessing effects of species composition on insect damage has been at the stand level rather than at the landscape level. We have demonstrated for these three insect system examples that mixedwood stands sustain lower defoliation, beetle damage, and tree mortality than conifer- or broadleaf-dominated stands. What about a mixed landscape composed of a mixture of conifer and broadleaf stands? Theoretically, the boundaries between such stands in a mixed landscape should provide similar benefits to those from a mixedwood stand, but the interiors of pure conifer and broadleaf stands should sustain levels of damage approaching that of pure stands. Yet there may be some landscape-level synergy that exceeds the effect of boundary conditions, depending on the mechanism of the reduced damage response, whether it involves other trophic levels (e.g., parasitoids), and if so, the mobility of those species. In one of the few related studies, Campbell et al. (2008) evaluated how radial growth reductions during a spruce budworm outbreak varied in response to the broadleaf content of surrounding forest landscapes (within a 1 km radius of the balsam fir stand centroid). Broadleaf content of surrounding landscapes entered into all significant regression models, explaining 12%–41% of the variance in budworm-caused growth reductions. Landscape broadleaf content had stronger relationships to growth reductions among stands than did elevation or insecticide spray history (Campbell et al. 2008). Further experimental study of insect damage as a function of insect population processes and location within mixed landscapes is worthy of future study.

A number of challenges and opportunities can be identified for managing mixedwood forests to mitigate insect damage and promote forest health in forests. Land ownership presents both challenges and opportunities, because management options for privately owned forests are often driven by factors that differ from those on public lands.

Approximately 85% and 77% of the forested lands in the northeastern US and mid-Atlantic regions, respectively, are in private ownership. Diverse ownership results in forests being managed (or not in some cases) for a variety of goals and not solely the production of sawlogs and pulpwood products (Shifley et al. 2014; Butler et al. 2016). Current condition of private forests is also important for future potential management strategies. Nearly half of the forested land in northeastern US forests is considered "degraded", based on low stocking densities and poor form of commercially desirable species and increased basal area of American beech and red maple as a result of exploitative harvesting, insect damage, and changing climate (Kosiba et al. 2018; Gunn et al. 2019). Additional interactions between forest management, altered disturbance regimes, increasing ungulate abundance, and introductions of invasive species have further contributed to forest degradation; however, adopting appropriate multi-aged mixedwood silvicultural systems that promote a greater diversity of tree species could reverse the erosion of ecological "memory" (sensu Webster et al. 2018) associated with forest degradation. Such silvicultural systems could enhance the combined adaptations of forest species that guide recovery following insect infestations and increase resistance and resilience to future infestations (Jactel et al. 2017; Kenefic et al. 2021).

Timber products markets also present some challenges and opportunities for managing mixedwood forests. Demand for softwood sawlogs and pulpwood products has decreased in many regions relative to pre-2008, although it strongly rebounded in 2020 and 2021. Global prices for pulpwood are relatively low, with abundant supply from international sources (e.g., Australia, Brazil, Chile). This has driven a recent reevaluation of short-rotation pine production in the southeastern and mid-Atlantic US for some landowners, with longer rotation mixedwood forest management as an option (Willis et al. 2019).

Opportunities also exist for using mixedwood systems in intensive forest management. Currently, a great majority of plantation forests consist of one or a few species. If the proportion of plantation forests expands in the future in some regions or on some ownerships, carefully designed mixedwood silvicultural systems could be integrated with strategies such as assisted migration to produce more resistant and resilient plantations. Such an approach may provide additional biodiversity and economic benefits associated with increased tree species and structural diversity (resulting from vertical stratification of hardwoods and softwoods) and improved stem quality if softwoods shade the boles of hardwoods and increase branch shedding.

Conclusions

Insect damage is now the dominant disturbance in forests in the northeastern and mid-Atlantic regions of North America; however, standing and downed deadwood are increasingly being recognized as very important ecologically and as improvements to the habitat for numerous biotic species, so there is a trade-off. Hence, there are some positives to these mortality events and the values and trade-offs involved, but a problem is the large-scale nature of mortality occurring across hundreds of thousands or millions of hectares. Associational resistance of host species often results in mixedwood stands being more resistant to insect infestations and incurring lower rates of tree and sapling mortality. Mechanisms vary among insect species but often involve dilution of preferred host trees and reduced visual or chemical apparency, higher density or diversity of natural enemies, especially parasitoids, or higher dispersal losses of insects in mixedwoods than in pure hardwood or softwood stands.

Forest inventory data, process-based productivity models, and carbon flux measurements for some forest types indicated that NPP and NEP are not significantly different among mixedwood stands and hardwood- or softwood-dominated stands (e.g., oak-dominated, mixedwood, and pine-dominated stands in the mid-Atlantic region).

Long-term inventory and flux data from insect-damaged stands indicate that ecosystem functioning parallels changes in structure and species composition and that carbon and hydrologic fluxes converge on those characterizing oak–pine mixedwood forests in that region. Although mixedwoods are not a panacea and characteristics of tree species and desired products must be considered, we believe that mixedwood management can play a substantive role in reducing insect damage of host species. The impetus toward ecological forestry and uneven-aged forest management that is occurring in many regions provides an opportunity for commercial mixedwood management at stand and landscape scales.

Acknowledgements

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