Advances in understanding and managing insect pests of forest trees

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1 Introduction

Forest ecosystems cover roughly one-third of the world's land base, providing vital contributions to people and the planet we inhabit (FAO, 2018). Boreal and temperate forests, which make up almost half of all forested land and include ~1.3 trillion trees (Crowther et al., 2015), are a major source of timber, biomass, and other ecosystem services including clean air and water, hunting, recreation, cultural identities, and global biodiversity and sustainability (Gauthier et al., 2015; Brecka et al., 2018). Through carbon sequestration and storage, forests are also increasingly recognized for mitigation of atmospheric concentrations of carbon dioxide (CO_2) (Dugan et al., 2018) that are contributing to a changing climate (IPCC, 2014). As carbon sinks,

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forests worldwide absorb the equivalent of ~2 billion tonnes of CO_2 each year (Köhl et al., 2015; FAO, 2018), and ~42% of that carbon is held in living tree biomass (Pan et al., 2011). The future of forests globally, however, is being threatened by a variety of factors including an increased rate of native disturbances due to a changing climate (Fettig et al., 2013a; Allen et al., 2015), and an increased frequency of invasive species introductions as global trade accelerates (Aukema et al., 2010; Brockerhoff and Liebhold, 2017). Disturbances that result in large amounts of tree mortality can reverse the role of forests from carbon sinks to carbon sources, at least in the short term until regrowth occurs (Hansen et al., 2015; Arora et al., 2016). In a rapidly changing climate, consequences of expansive tree mortality could also include altered successional trajectories with long-term type conversions and negative impacts to biodiversity as ecosystem tipping points are crossed in no-analog climates (Fox, 2007; Anderegg et al., 2013; Vose et al., 2018).

In boreal and temperate forests, disturbances caused by native and non-native invasive insects are among the most important mediators of tree mortality (Berner et al., 2017; Liebhold et al., 2017; Mezei et al., 2017). Although native herbivorous insects are considered integral components of forest ecosystems (Mattson and Addy, 1975) and the majority cause no economic damage (Raffa et al., 2015), species within a few genera are considered pests when outbreaks interfere with land management objectives and cause significant ecological and economic impacts (Cooke et al., 2007; Raffa et al., 2009). Globally, between 2003 and 2012, >70 million ha of boreal and temperate forests were affected by insect pests, with more than half occurring in North and Central America (van Lierop et al., 2015).

Many traits that influence forest insect population success are temperature dependent and warming temperatures are causing range expansions and altered outbreak frequencies (Weed et al., 2013; Pureswaran et al., 2018). Insects not considered pests in their native habitats can become pests when introduced into new habitats as they respond to enemy-free (Keane and Crawley, 2002) and defense-free environments (Showalter et al., 2018). Climatic changes are expected to result in continued alterations in the frequency and distribution of native and invasive insect outbreaks (Logan et al., 2003; Forrest, 2016), in addition to stress-related changes in forest composition and structure that influence suitability to insect predators (Kolb et al., 2016; Marini et al., 2017; Lantschner et al., 2019). The interacting effects of climate change on insects and host trees coupled with increasing arrival rates of non-native insects globally (McCullough et al., 2006; Brockerhoff and Liebhold, 2017) are making management of boreal and temperate forests for timber and other ecosystem services increasingly uncertain and challenging. We review current information and key issues for predicting distributions in a changing climate, and for managing native (Tables 1 and 2)

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Table 1 Bark beetles (Coleoptera: Curculionidae, Scolytinae) noted in their native ranges for causing conifer tree mortality in Northern Hemisphere boreal and temperate forests

Common name	Scientific name	Native continent	Common host(s)
Arizona fivespined ips	*Ips lecontei*	North America	*Pinus ponderosa*
California fivespined ips	*Ips paraconfusus*	North America	*P. attenuata, P. coulteri, P. lambertiana, P. ponderosa, P. radiata*
Chinese white pine beetle	*Dendroctonus armandi*	Asia	*P. armandii*
Douglas-fir beetle	*Dendroctonus pseudotsugae*	North America	*Pseudotsuga menziesii,* occasionally *Larix occidentalis*
Eastern fivespined ips	*Ips grandicollis*	North America	*P. echinata*, *P. elliottii*, *P. taeda*, *P. virginiana*
Eastern larch beetle	*Dendroctonus simplex*	North America	*Larix laricina*
Fir engraver	*Scolytus ventralis*	North America	*Abies concolor*, *A. grandis*, *A. magnifica*
Great spruce bark beetle	*Dendroctonus micans*	Europe, Asia	*Pi. abies; P. sylvestris*
Jeffrey pine beetle	*Dendroctonus jeffreyi*	North America	*P. jeffreyi*
Larger eight-toothed European spruce bark beetle (= European spruce beetle)	*Ips typographus*	Europe, Asia	*Picea abies*, *Pi. orientalis*, *Pi. yezoensis*, occasionally *P. sylvestris*
Larger Mexican pine beetle	*Dendroctonus approximatus*	North America	*P. engelmannii, P. leiophylla, P. ponderosa*
Mountain pine beetle	*Dendroctonus ponderosae*	North America	*P. albicaulis*, *P. contorta*, *P. flexilis*, *P. lambertiana*, *P. monticola*, *P. ponderosa*
Northern spruce engraver	*Ips perturbatus*	North America	*Pi. engelmannii, Pi. glauca, Pi. x lutzii, occasionally Pi. mariana*
Pine engraver	*Ips pini*	North America	*P. banksiana, P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*, *P. resinosa, P. strobus*
Pinyon ips	*Ips confusus*	North America	*P. edulis*, *P. monophylla*
Roundheaded pine beetle	*Dendroctonus adjunctus*	North America	*P. arizonica*, *P. engelmannii*, *P. flexilis*, *P. leiophylla*, *P. ponderosa*, *P. strobiformis*
Sixspined ips	*Ips calligraphus*	North America	*P. echinata, P. elliotti, P. ponderosa, P. taeda, P. virginiana*
Six-toothed bark beetle	*Ips sexdentatus*	Europe, Asia	*P. heldreichii, P. nigra*, *P. pinaster*, *P. sylvestris*, *Pi. orientalis*

(*Continued*)

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Table 1 (*Continued*)

Common name	Scientific name	Native continent	Common host(s)
Southern pine beetle	*Dendroctonus frontalis*	North America	*P. echinata, P. engelmannii, P. leiophylla, P. ponderosa, P. rigida, P. taeda, P. virginiana*
Spruce beetle	*Dendroctonus rufipennis*	North America	*Pi. engelmannii, Pi. glauca, Pi. pungens, Pi. sitchensis*
Western balsam bark beetle	*Dryocoetes confusus*	North America	*A. lasiocarpa*
Western pine beetle	*Dendroctonus brevicomis*	North America	*P. coulteri, P. ponderosa*

and invasive (Table 3) forest insects that are considered pests in boreal and temperate forests of the northern hemisphere. Five case studies highlight recent strategies being applied to mitigate forest insect–caused tree mortality (Fig. 1; Section 7).

2 Advances in understanding and predicting native and invasive forest insect responses to climate change

The timing of seasonal life history events (i.e. phenology) is critical for insects, especially in boreal and temperate regions of the world. Strategies are required to survive harsh winters, and the relatively short growing season demands that organisms prepare to feed and reproduce as soon as temperatures become sufficiently warm (Bale et al., 2002). Forest insects have adapted multiple thermally dependent phenological strategies to survive and persist in harsh climates including development rates and thermal thresholds, diapause (a dormant physiological state entered to survive harsh conditions and increase cohort synchrony), and cold-hardening (increased cold tolerance through acclimation and metabolic processes) (Bentz and Jönsson, 2015). These traits, in addition to interactions with host trees and community and symbiotic associates, will determine species- and location-specific responses of forest insects to a changing climate (Netherer and Schopf, 2010; Weed et al., 2013). In northern latitudes, phenological traits of insects have influenced range limits where, despite the availability of host plants, climates were historically too cool to allow completion of life cycles or permit overwinter survival (Safranyik and Wilson, 2006). Northern latitudes are warming more rapidly than global means (IPCC, 2014) and observations of movement to new, thermally suitable environments is the most noticeable response of organisms to climate warming (Chen et al., 2011).

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Table 2 Defoliator species that can cause extensive tree mortality in their native habitats in Northern Hemisphere boreal and temperate forests

Common name	Scientific name	Native continent	Common host(s)
Asian gypsy moth	*Lymantria dispar asiatica* Lepidoptera: Erebidae	Asia	*Acer* spp., *Alnus* spp., *Betula* spp., *Larix* spp., *Picea* spp., *Pinus* spp., *Populus* spp., *Quercus* spp.
Autumnal moth	*Epirrita autumnata* Lepidoptera: Geometridae	Europe	*Betula pubescens*
Balsam fir sawfly	*Neodiprion abietis* Hymenoptera: Diprionidae	North America	*Abies balsamea, Picea glauca, Pi. mariana*
European gypsy moth	*Lymantria dispar dispar* Lepidoptera: Erebidae	Europe	*Acer* spp., *Alnus* spp., *Betula* spp., *Populus* spp., *Quercus* spp.
European pine sawfly	*Neodiprion sertifer* Hymenoptera: Diprionidae	Europe	*Pinus* spp.
Forest tent caterpillar	*Malacosoma disstria* Lepidoptera: Lasiocampidae	North America	*Acer saccharum, Populus* spp.
Hemlock looper	*Lambdina fiscellaria* Lepidoptera: Geometridae	North America	*Abies balsamea, Acer saccharum, Betula papyrifera, Picea glauca, Tsuga canadensis*
Jack pine budworm	*Choristoneura pinus* Lepidoptera: Tortricidae	North America	*Pinus banksiana*
Larch bud moth	*Zeiraphera diniana* Lepidoptera: Tortricidae	Europe	*Larix decidua, Pinus cembra*
Nun moth	*Lymantria monacha* Lepidoptera: Erebidae	Europe	*Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp.
Pine moth	*Dendrolimus spectabilis* Lepidoptera: Lasiocampidae	Asia–Japan	*Pinus densiflora, P. thunbergii*
Pine processionary moth	*Thaumetopoea pityocampa Lepidoptera: Thaumetopoeidae*	Europe	*Pinus* spp.
Redheaded pine sawfly	*Neodiprion lecontei* Hymenoptera: Diprionidae	North America	*Pinus* spp.
Scarce umber	*Agriopis aurantiaria* Lepidoptera: Geometridae	Europe	*Betula* spp., *Quercus* spp., *Salix* spp., *Ulmus* spp.
Siberian silk moth/white-lined silk moth	*Dendrolimus sibiricus/ superans* Lepidoptera: Lasiocampidae	Northern Asia	*Abies sibirica, Pinus sibirica, Picea* spp., *and Larix* spp.
Spruce budworm	*Choristoneura fumiferana* Lepidoptera: Tortricidae	North America	*Abies balsamea, Picea glauca, Pi. mariana*
Western spruce budworm	*Choristoneura freemani* Lepidoptera: Tortricidae	North America	*Picea engelmanni, Pseudotsuga menziesii*
Winter moth	*Operophtera brumata* Lepidoptera: Geometridae	Europe	*Betula pubescens*
Yellowheaded spruce sawfly	*Pikonema alaskensis* Hymenoptera: Tenthredinidae	North America	*Picea* spp.

Table 3 Examples of invasive forest insect pests that cause significant damage in Northern Hemisphere boreal and temperate forests

Common name	Scientific name	Native continent	Introduced range	Hosts	Selected References
Asian gypsy moth	*Lymantria dispar asiatica* Vnukovskij; *Lymantria dispar japonica* (Motchulsky) (Lepidoptera: Erebidae)	Asia	Russia	*Quercus, Betula, Alnus, Salix, Prunus, Larix, Pseudotsuga*	Pogue and Schaefer (2007)
Asian longhorned beetle	*Anoplophora glabripennis* Motchulsky (Coleoptera: Cerambycidae)	Asia	North America, Europe	*Acer, Populus, Salix*, others	Hu et al. (2009), Dodds and Orwig (2011)
Balsam woolly adelgid	*Adelges piceae* Ratzeburg (Hemiptera: Adelgidae)	Europe	North America	*Abies*	Smith and Nicholas (1998)
Beech scale + beech bark disease	*Cryptococcus fagisuga* Lindinger (Hemiptera: Eriococcidae)+ *Nectria coccinea* var. *faginata*, *Nectria galligena*	Europe	North America	*Fagus*	Houston (1994)
Blue gum chalcid	*Leptocybe invasa* Fisher & La Salle (Hymenoptera: Chalcidae)	Australia	Africa, Asia, Europe	*Eucalyptus, Corymbia*	Mendel et al. (2004), Zheng et al. (2014)
Chestnut gall wasp	*Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae)	Asia	Europe and North America	*Castanea*	Rieske (2007), Battisti et al. (2014)
Citrus longhorned beetle	*Anoplophora chinensis* Forster (Coleoptera: Cerambycidae)	China, Korea, Japan	Europe	*Acer, Citrus, Populus, Ulmus,* others	Hérard and Maspero (2019)
Coconut hispine beetle	*Brontispa longissimi* (Gestro) (Coleoptera: Chrysomelidae)	Indonesia	China	*Areca, Cocos, Elaeis, Metroxylon, Phoenix*	Nakamura et al. (2006)
Cypress aphid	*Cinara cupressi sensu lato* (Hemiptera: Aphididae)	North America	Africa, Europe	*Cupressus*, *Juniperus, Thuja*	Watson et al. (1999), Mendel et al. (2016)
Cypress jewel beetle	*Lamprodila* (*Palmar*) *festiva* (L.) (Coleoptera: Buprestidae)		Russia	*Chamaecyparis*, *Cupressus*, *Juniperus, Thuja*	Volkovitsh and Karpun (2017)
Emerald ash borer	*Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae)	Asia	North America, Europe, Russia	*Fraxinus, Olea*	Herms and McCullough (2014)
Eucalyptus leaf weevils	*Gonipterus* spp. (Coleoptera: Curculionidae)	Australia	Africa	*Eucalyptus*	Hurley et al. (2016)

Eucalyptus longhorned beetle	*Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae)	Australia	North America, Israel, Turkey, Europe	*Eucalyptus*	Scriven et al. (1986), Paine (2016)
European gypsy moth	*Lymantria dispar dispar* (L.) (Lepidoptera: Erebidae)	Europe	North America	*Quercus*, others	Davidson et al. (2001), Tobin and Liebhold (2011)
Fall webworm	*Hyphantria cunea* Drury (Lepidoptera: Erebidae)	North America	China, Europe	*Betula, Carya, Platanus, Salix, Ulmus,* others	Szalay-Marzso (1971), Yang et al. (2008)
Four-eyed fir bark beetle	*Polygraphus proximus* Blandford (Coleoptera: Curculionidae: Scolytinae)	China, Korea, Russian Far East	European Russia	*Abies, Larix, Picea*	Baranchikov et al. (2010)
Hemlock woolly adelgid	*Adelges tsugae* (Annand) (Hemiptera: Adelgidae)	Japan	North America	*Tsuga*	Vose et al. (2013)
Loblolly pine mealybug	*Oracella acuta* (Lobdell) (Hemiptera: Pseudococcidae)	USA	China	*Pinus*	Chen et al. (2017), Lu and Sun (2017)
Pine needle hemiberlesian scale	*Hemiberlesia pitysophila* Takagi (Hemiptera: Diaspididae)	Japan	China	*Pinus*	Feng et al. (2009)
Pine wood nematode + pine wilt disease	*Monochamus* spp. (Coleoptera: Cerambycidae) + *Bursaphelenchus xylophilus*	North America	Asia and Europe	*Pinus*	Lee et al. (2017)
Polyphagous shot hole borer + fusarium dieback	*Euwallacea whitfordiodendrus* and *E. kuroshio* (Coleoptera: Curculionidae: Scolytinae) + *Fusarium* spp., *Acremonium* spp., *Graphium* spp.	Asia	North America, Israel	*Acer, Alnus, Platanus, Populus, Salix,* others	Eskalen et al. (2013), Lynch et al. (2016), Gomez et al. (2018), Coleman et al. (2019)
Red turpentine beetle	*Dendroctomus valens* (LeConte) (Coleoptera: Curculionidae: Scolytinae)	North and Central America	China	*Pinus, Larix, Picea*	Sun et al. (2013)
Redbay ambrosia beetle + laurel wilt	*Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae) + *Raffealea lauricola*	India, Japan, Myanmar, and Taiwan	North America	*Persea, Sassafras*, others	Fraedrich et al. (2008), Hughes et al. (2015)
Siberian silk moth	*Dendrolimus sibiricus* Tschetv. (Lepidoptera: Lasiocampidae)	Siberia, China, North Korea	Russia, Central Europe	*Pinus, Larix, Abies, Picea*	Kirichenko et al. (2009), Kononov et al. (2016)

(*Continued*)

Table 3 (*Continued*)

Common name	Scientific name	Native continent	Introduced range	Hosts	Selected References
Sirex woodwasp	*Sirex noctilio* (F.) (Hymenoptera: Siricidae)	Eurasia, North Africa	Australia, New Zealand, North and South America, South Africa	*Pinus*	Haavik et al. (2015)
Smaller European elm and banded elm bark beetles + Dutch elm disease	*Scolytus multistriatus* (Marsham) and *S. schevyrewi* (Semenov) (Coleoptera: Curculionidae: Scolytinae) + *Ophiostoma ulmi, Ophiostoma novo-ulmi*	Europe	North America, New Zealand	*Ulmus*	Brasier and Buck (2001), Negrón et al. (2005), Jacobi et al. (2013)
Spotted lantern fly	*Lycorma delicatula* (White) (Hemiptera: Fulgoridae)	Northern China	North America	*Acer, Ailanthus, Malus, Populus, Prunus,* others	Dara et al. (2015)
Thuja shoot borer	*Phloeosinus aubei* (Perris)	Mediterranean region	Central Europe, expanded range	*Thuja*	Bozsik and Szőcs (2017)
Walnut twig beetle + thousand cankers disease	*Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae: Scolytinae) + *Geosmithia morbida*	North America	North America-expanded range, Europe-Italy	*Juglans, Pterocarya*	Tisserat et al. (2009), Seybold et al. (2016, 2019)
Western conifer seedbug	*Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae)	North America	Europe, Japan, North America-expanded range	*Abies, Pinus, Pseudotsuga, Tsuga*	McPherson et al. (1990), Ishikawa and Kikuhara (2009), Lesieur et al. (2019)
Winter moth	*Operophtera brumata* L. (Lepidoptera: Geometridae)	Europe	North America	*Acer, Betula, Malus, Ostrya, Quercus, Tilia, Ulmus*	Simmons et al. (2014)
Yellow phoracantha	*Phoracantha recurva* Newman (Coleoptera: Cerambycidae)	Australia, Papua New Guinea	North America	*Eucalyptus*	Hanks et al. (1997), Paine (2016)

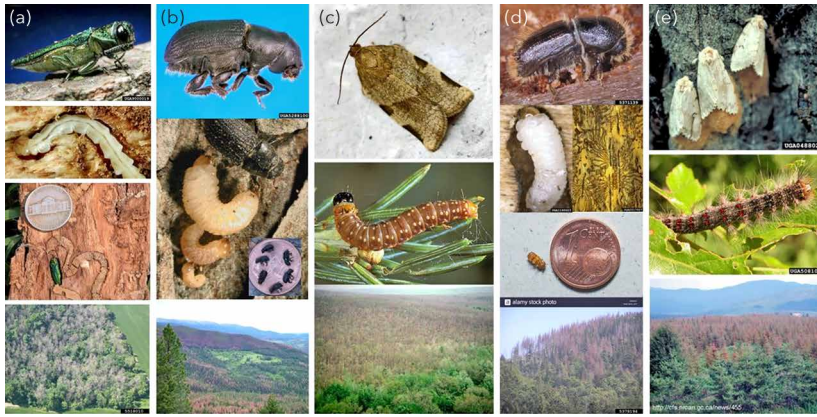

Figure 1 Adult and larval form, and forest ecosystem impact of insects described in case studies (Section 7). (a) emerald ash borer, (b) mountain pine beetle, (c) spruce budworm, (d) European spruce beetle, and e) European gypsy moth. See Tables 1–3 for additional information on each species. Photo credits: B. Bentz, M. Ayres; Bugwood.org – D. Adam, D. Cappaert, G. Csoka, W. Ciesla, E. Day, G. Ghent, T. Kimoto, F. Lakatos, M. Zubrik.

2.1 Observed and predicted responses to changing climate

As might be expected, warming winter temperature is most often cited as the key environmental factor influencing observed native forest insect population range shifts or expansions northward (Table 4). Warming spring temperatures that positively influence defoliator larval feeding to be synchronous with bud break of host trees can also be a contributing factor to range shifts (Table 4). While it is clear that warming has allowed some native forest insect populations to expand northward, many populations have also exhibited increased duration and intensity of population outbreaks within historic geographic ranges as a result of the combined effects of drought, increased storms that result in stressed host trees, and warming summer and winter temperatures that reduce generation time and increase population survival (e.g., Berg et al., 2006; Jactel et al., 2012; Flower et al., 2014; Weed et al., 2015; Kolb et al., 2016; Berner et al., 2017; Hart et al., 2017; Marini et al., 2017; Fettig et al., 2019; Ward et al., 2019). Although range expansions or shifts are occurring and warming temperatures have generally been favorable for forest insects, climate change may also restrict native and invasive population success (Forrest, 2016). Indeed, recent observations show that long-term native and invasive population spatial synchrony and outbreak cycles have been disrupted, resulting in negative impacts to forest insect populations (Esper et al., 2006; Johnson et al., 2010; Haynes et al., 2014; Cooke and Roland, 2018).

Table 4 Observed recent range expansions of forest insect species in their native continents associated with abiotic factors. See Tables 1 and 2 for additional species information.

Common name	Native continent	Inciting abiotic factor(s)	References
Autumnal moth	Europe	Warming mean and winter temperature	Jepsen et al. (2008)
Mountain pine beetle	North America	Warming winter temperature	Carroll et al. (2004), Stahl et al. (2006), Sambaraju et al. (2012)
Pine processionary moth	Europe	Warming winter temperature	Battisti et al. (2005), Netherer and Schopf (2010)
Scarce umber	Europe	Warming spring temperature	Jepsen et al. (2011)
Siberian silk moth	Northern Asia	Sum of temperatures >0°C, drought	Kharuk et al. (2018)
Southern pine beetle	North America	Warming winter temperature	Weed et al. (2013), Dodds et al. (2018)
Spruce budworm	North America	Warming spring and winter temperature	Candau and Fleming (2005)
Western spruce budworm	North America	Warming year-round temperatures	Thomson and Benton (2007), Maclauchlan et al. (2018), Régnière and Nealis (2019)
Winter moth	Europe	Warming mean and winter temperature	Jepsen et al. (2008)

As climate change is expected to continue (IPCC, 2014), numerous studies have used transplant experiments and a variety of statistical and process-based models, in association with forecasted temperatures based on Global Climate Models, to predict population success and range expansions beyond historical distributions. With a few exceptions, range expansion northward and increased population success were predicted for most species (Table 5). European gypsy moth (*Lymantria dispar dispar*) expansion was predicted to be limited by winter temperatures in North America where it is invasive, and also in Europe where it is native. Process-based models predicted northward expansions for spruce budworm (*Choristoneura fumiferana*), western spruce budworm (*C. freemani*), and mountain pine beetle (*Dendroctonus ponderosae*), but also southern range retractions (Table 5). In contrast with statistical or correlative models, process-based models include species-specific details on thermally dependent traits that drive seasonality and population success, and in all three species excessive warming at southern range limits was predicted to disrupt diapause and developmental traits that have evolved to synchronize individuals with each other, their hosts, and seasonal environments (Régnière et al., 2012; Bentz et al., 2019; Régnière and Nealis, 2019).

Correlative or statistical approaches between insect occurrence and climate variables, which have been most often used to project future

Table 5 Predictions of range expansion and population success for native and invasive forest insect species in a changing climate. See Tables 1–3 for additional species information

Common name	Prediction(s)	References
Emerald ash borer	Range expansion northward in both North America and Europe where it is invasive	Sobek-Swant et al. (2012b), Valenta et al. (2017), Cuddington et al. (2018)
European gypsy moth	Limited by winter cold in North America where it is invasive, except when insulated by snow cover; limited by winter cold within its native range in Europe	Vanhanen et al. (2007), Régnière et al. (2009), Yasyukevich et al. (2015), Fält-Nardmann et al. (2018a), Streifel et al. (2019)
European pine sawfly	Range expansion northward in Europe	Virtanen et al. (1996)
Hemlock woolly adelgid	Model results are mixed regarding susceptibility to cold and potential range expansion northward in North America where it is invasive	Dukes et al. (2009), Fitzpatrick et al. (2012), McAvoy et al. (2017)
European spruce beetle	Increased population success through reduced generation time in Europe and in North America where it could become invasive; drought and severe storms increase outbreak frequency; increased disturbance areas	Jönsson et al. (2009, 2011), Økland et al. (2015), Seidl and Rammer (2017), Bentz et al. (2019)
Mountain pine beetle	Range shift northward in North America; increased population success at high elevations due to reduction in generation time; range contraction of historical distribution in United States due to disruption of seasonality; range expansion southward in North America; high establishment potential in parts of Europe	Bentz et al. (2010, 2016, 2019), Safranyik et al. (2010), Weed et al. (2015), Buotte et al. (2016), Sidder et al. (2016), Cooke and Carroll (2017)
Nun moth	Range expansion northward and eastward in Europe	Vanhanen et al. (2007), Yasyukevich et al. (2015), Fält-Nardmann et al. (2018b)
Red turpentine beetle	Population success in predicted invaded areas of Southern Hemisphere; expansion of populations in China where it is invasive	He et al. (2015), Lantschner et al. (2017)
Redbay ambrosia beetle	Range expansion northward in North America where it is invasive	Formby et al. (2018)
Sirex woodwasp	Range expansion in areas of Australia, Brazil, and northeastern North America where it is invasive	Carnegie et al. (2006), Lantschner et al. (2014), Ireland et al. (2018)
Southern pine beetle	Range expansion northward in North America	Lesk et al. (2017)
Spruce beetle	Increased population success through reduced generation time in North America in areas with suitable host trees	Bentz et al. (2010), DeRose et al. (2013)

(*Continued*)

Table 5 (*Continued*)

Common name	Prediction(s)	References
Spruce budworm	Range expansion northward in parts of North America (limited by thermal energy for life cycle completion); range contraction in southern United States due to diapause disruption	Gray (2008), Candau and Fleming (2011), Régnière et al. (2012), Pureswaran et al. (2015)
Western spruce budworm	Range expansion northward; less population success at lower latitudes (except at high elevations) due to exhaustion of energy reserves and mortality of overwintering larvae	Régnière and Nealis (2019)

range distributions, can provide estimates in the near-term but they do not adequately describe the nonlinear and evolved nature of insect responses to temperature, often do not include year-round temperature extremes that can influence forest insect success, and can be hampered by poor data on pest population distributions (Régnière et al., 2012; Barredo et al., 2015; Thompson et al., 2017; Mech et al., 2018). To adequately predict and manage for future responses of forest insects to a rapidly changing climate, process-based models based on species-specific phenological responses are needed. Quantification of thermal effects on complex nonlinear relationships among forest insects, their host trees, and community associates, including predators and microbial symbionts, will also enhance predictions (Dukes et al., 2009; Addison et al., 2015; Schwartzberg et al., 2014).

2.2 Plasticity and adaptive potential in a changing climate

Variation within and among forest insect populations in thermally regulated traits can potentially provide adaptive capacity to changing climatic conditions. Phenotypic plasticity, an organism's ability to adjust its phenotype in response to changes in environmental conditions, allows for higher fitness than if the trait was fixed, and populations with sufficient plasticity may persist in a rapidly changing environment in the short term without adaptation (Gienapp et al., 2008). Plasticity in thermally regulated traits has been demonstrated in some forest insect species including the European pine sawfly (*Neodiprion sertifer*) (Veteli et al., 2005), nun moth (*Lymantria monacha*), autumnal moth (*Epirrita autumnata*), European gypsy moth (in native and invaded ranges) (Keena, 2016; Fält-Nardmann et al., 2016, 2017; Thompson et al., 2017), mountain pine beetle (Bentz et al., 2011; Bentz and Hansen, 2018; McManis et al., 2018), European spruce beetle (Schroeder and Dalin, 2017), and the emerald ash borer (*Agrilus planipennis*) (Sobek-Swant et al., 2012a) and hemlock woolly

adelgid (*Adelges tsugae*) (Butin et al., 2005; Lombardo and Elkinton, 2017) in invaded areas of North America. There are limits to plasticity, however, and long-term persistence *in situ* will require adaptations that occur through genetic evolution. Empirical data showing heritable genetic adaptation to rapidly changing conditions, however, are rare in insect pests (Garnas, 2018). In the one documented case for forest insects, van Asch et al. (2013) showed a genetic shift in the nun moth, from 2000 to 2010, to hatch their eggs later in spring to ensure that feeding larvae remain synchronized with bud break of host oaks. Recent northward range expansion of mountain pine beetle in Canada has also been associated with signals of directional selection on metabolic and cellular processes that may allow increased tolerance to cold temperatures (Janes et al., 2014).

3 Advances in managing for resistance in native and invasive forest insect systems

Tree resistance to herbivory involves a variety of physical and chemical defenses that are under genetic and environmental control. Harnessing resistance is key for future management of both native and alien invasive insect species (Telford et al., 2015). A framework was recently developed that is based on an in-depth analysis of factors associated with recurring failures in the long-term management of tree-killing, alien invasive insects in forest environments (Showalter et al., 2018). The analyses revealed that because alien invasive insects encounter defense-free spaces in their new environments, the evolutionarily naïve host trees are generally incapable of mounting adequate resistance responses. Top-down control by both native and introduced natural enemies can also be hampered, at times limiting the efficacy of biological control. Even the most undefended host populations, however, almost always include individuals that are capable of resisting attack. Such resistance need not be absolute (immunity), but sufficient to ensure survival and reproduction of the target host. Given survival, either natural selection can act directionally upon the traits conferring resistance in the long run, or modern approaches can be developed, including tree improvement programs, that are increasingly capable of rapidly selecting and augmenting tree defenses (Sniezko and Koch, 2017). In the latter case, improved trees could then be used for resilient plantings.

The practicality of tree-for-planting improvement programs is becoming more evident, as selection of resistant trees can be accelerated by using non-destructive resistance screening techniques based on modern -omics approaches. For example, intraspecific variability in host resistance can be detected by using a metabolomics-derived approach that includes infrared or Raman spectroscopic fingerprinting of phenolic extracts. Analysis of the

chemical fingerprints is performed by using chemometric methods, which may include statistical approaches such as soft independent modeling of class analogy, principal components analysis, or, more generally, artificial intelligence tools such as artificial neural networks and support vector machines. Such analytical techniques are simply meant to classify plants as resistant or susceptible without reference to a specific mechanism (Conrad et al., 2014; Conrad and Bonello, 2016; Villari et al., 2017). Genomics and transcriptomics approaches have also been shown to be very promising in this respect (Harper et al., 2016).

Interspecific variability can also be helpful in understanding mechanisms of resistance that could then be developed into phenotyping tools for specific alien pest species. For example, little host resistance (but greater than complete susceptibility) appears to be available against emerald ash borer in North American ash species (Koch et al., 2015). Comparisons between North American naïve ash species and co-evolved, resistant Asian species such as Manchurian ash (*Fraxinus mandschurica*) have highlighted differences in the way they respond to emerald ash borer that are beginning to point to specific mechanisms that could be used for phenotyping. However, since interspecific comparisons can be confounded by genetic variation in unrelated traits, it is important to control for phylogeny. In the case of the emerald ash borer, the most relevant comparison has been between Manchurian ash (resistant) and black ash (*F. nigra*), the latter a highly susceptible North American species that belongs to the same section of *Fraxinus* as Manchurian ash (Wallander, 2008). Rigsby et al. (2015, 2016) have shown that resistance in Manchurian ash is characterized by higher activities of enzymes that appear to function by oxidative 'activation' of constitutive phenolics into quinones, among other mechanisms. Thus, screening for quinone generation may become a non-destructive tool to select more resistant North American ash individuals.

As would be expected from an evolutionary perspective, host tree resistance has been observed more frequently in native than alien invasive forest insect systems. Perhaps the most successful case of harnessing natural genetic variation for native species management is spruce (*Picea*) resistance to the white pine weevil (*Pissodes strobi*), a phloem feeder in regeneration-age spruce and white pines in North America. Heritable genetic variation in resistance to the white pine weevil has been well documented for multiple spruce species in western Canada (Kiss and Yanchuk, 1991; King et al., 2011). Evolved traits in spruce to weevil herbivory include stone cells that act as a physical barrier to feeding larvae and can slow development, thereby enhancing the toxic impacts of resin terpenes (Alfaro et al., 2004; Whitehill et al., 2019). Several seed orchards with resistant spruce for use in reforestation plantations have been established (Alfaro et al., 2013).

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In other systems, genetic variability in resistance to native insects has been identified, although tree breeding programs have not yet been developed. Recent research suggests high levels of genetic variation in susceptibility to the large pine weevil (*Hylobius abietis*), a pest of regeneration-age conifers in Europe, among Norway spruce (*Picea abies*) in southern Sweden (Zas et al., 2017) and maritime pine (*P. pinaster*) across its range (López-Goldar et al., 2018). Interestingly, in the latter study, inducibility of host chemical defenses was a critical factor in predicting resistance among host populations, whereas constitutive levels were not. Naturally occurring resistance of white spruce (*Pi. glauca*) to spruce budworm has also been documented (Daoust et al., 2010), and linked to the content of several specialized metabolites in spruce foliage (Delvas et al., 2011). Differences in gene expression and associated constitutive levels of the compounds were observed between white spruce individuals from different geographic regions with different intensities of historical spruce budworm outbreaks, suggesting that the traits are under positive selection (Parent et al., 2017). *Intraspecific* genetic variability was found among lodgepole pine (*Pinus contorta*) genotypes that were either attacked or not attacked by mountain pine beetle (Yanchuk et al., 2008), and *interspecific* variability in resistance was recently demonstrated where mountain pine beetle–caused mortality of *P. flexilis* was extensive, but absent in co-occurring *P. longaeva* of similar size (Bentz et al., 2017). The quantity and composition of constitutive specialized metabolites of *P. longaeva* phloem may play a role in resistance to mountain pine beetle attack and offspring production (Eidson et al., 2017, 2018). These research results suggest that rapid, non-destructive spectrometric screening tools could be developed, with immediate benefits to tree breeding programs.

4 Advances in native bark beetle monitoring and management

Bark beetles are important disturbance agents in conifer forests of boreal and temperate ecosystems, and several notable species are capable of causing significant amounts of tree mortality (Table 1). Trees of all species, ages, and size classes may be colonized and killed, but each bark beetle species exhibits unique host preferences, life history traits, and impacts. In recent years, climate change has contributed to some bark beetle outbreaks and range expansions in North America and Europe due to shifts in temperature and precipitation that influence both the beetles and their hosts (Table 4) (Section 2.1).

Bark beetles are part of the natural ecology of conifer forest ecosystems, important to proper functioning as they regulate certain aspects of primary production, nutrient cycling, and ecological succession. To that end, some level of tree mortality is desirable and often results in a mosaic of forest structure

and composition that increases resistance and resilience to other disturbances. However, this varies from the ecological, economic, and social impacts of outbreaks, which can be significant (Morris et al., 2017). As a result, substantial basic and applied research has been devoted to the development of tools and tactics for mitigating undesirable levels of tree mortality attributed to bark beetles. Direct control involves short-term tactics designed to address current infestations by manipulating beetle populations, and often includes the use of sanitation harvests, semiochemicals (i.e. chemicals released by one organism that elicit a response, usually behavioural, in another organism), insecticides, or a combination of these and other treatments. Indirect control is preventive, and designed to reduce the probability and severity of future infestations by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and altering tree age classes, structure, and composition (Fettig and Hilszczański, 2015). Below, we provide a basic understanding of current and evolving management strategies. We encourage the reader to delve deeper into the literature cited and review the case studies on mountain pine beetle (Section 7.2) and larger eight-toothed European spruce bark beetle (= European spruce beetle), *Ips typographus* (L.) (Section 7.4), the most significant species in North America and Europe, respectively.

4.1 Survey and detection

Several methods are available to determine the distribution and severity of bark beetle infestations ranging from trapping programs to detect and monitor populations, to simple ground-based surveys, to a broad array of aerial surveys focused on detection of dead and dying trees (Fettig and Hilszczański, 2015). The most common method in North America incorporates the use of aircraft equipped with digital sketch-mapping systems (Fig. 2). In addition to showing the observer's position on a digital map, sketch mapping allows for real-time acquisition of data at lower costs (often <$ 1 USD/ha) than other survey methods. However, flying presents unique risks and considerable variability has been observed in data sketched by different observers. To address these concerns, recent research has focused on the utility of remotely sensed data obtained from satellites (Wulder et al., 2012) as the number and types of remote-sensing instruments have increased and image processing capabilities have greatly improved (Abdullah et al., 2019). The use of drone aircraft equipped with high-definition sensors and photographic equipment offers a new platform for survey and detection. Working in the central and southern Sierra Nevada, USA, Koontz et al. (2018) used drones to study the influence of spatial variability in forest structure on tree mortality attributed to western pine beetle (*D. brevicomis*). It is likely

Figure 2 Digital sketch-mapping systems are commonly used during aerial surveys of forest insect impact in North America. Photo credit: D. Wittwer, Forest Health Protection, USDA Forest Service.

that drones will play a larger role in the survey and detection of bark beetle infestations in the future.

4.2 Risk and hazard rating

Several risk and hazard rating systems are available to identify stands or forests that foster initiation and/or spread of bark beetle infestations (Fettig and Hilszczański, 2015). Most bark beetle species capable of causing extensive levels of tree mortality exhibit a preference for larger-diameter trees growing in high-density stands with a high percentage of host type (Fettig et al., 2007), and therefore such variables serve as a foundation for many risk and hazard rating

systems. The accuracy of risk and hazard rating systems are influenced by many factors, and their refinement remains an important research priority as climate change seems to be influencing these relationships (Morris et al., 2017).

4.3 Direct control

Bark beetles have been the focus of direct control dating back to the 1700s. For example, the Royal Society of Sciences at Göttingen, Germany, established an award to recognize the best proposal for management of European spruce beetle in the mid-eighteenth century. In short, a successful direct control program requires prompt and thorough applications of the most appropriate tactics. However, as with indirect control, implementation is often dictated by more practical concerns such as resource availability (e.g. budget, time, personnel, and equipment), market conditions, market conditions, as well as equipping, logistical, and social constraints (Mattor et al., 2019).

4.3.1 Acoustics

Bark beetles use acoustics in a variety of behaviors, including territoriality (Rudinsky et al., 1976), mate recognition (Rudinsky and Michael, 1973), and predator escape (Lewis and Cane, 1990). In recent years, a renewed interest in the study of bark beetle acoustics may lead to novel management tools (Hofstetter et al., 2019). For example, Aflitto and Hofstetter (2014) demonstrated in laboratory studies that attacks on logs by southern pine beetle (*D. frontalis*) and western pine beetle were reduced by certain acoustic signals.

4.3.2 Biological control

Natural enemies are important in regulating bark beetle populations and have potential utility in biological control programs. In China, mass rearing and release of *Rhizophagus grandis*, a predatory beetle native to Eurasia, has been implemented in response to the introduction of the red turpentine beetle (*D. valens*) (Yang et al., 2014). *Rhizophagus grandis* is also used for management of the great spruce beetle (*D. micans*) in Europe where recent research focuses on how phenological relationships between predator and prey may be impacted by climate change (Gent et al., 2017). Research from North America indicates that conservation and supplemental feeding of natural enemies may enhance biocontrol efforts. For example, supplemental feeding of parasitoids of the southern pine beetle with an artificial diet consisting largely of sucrose increased their longevity and fecundity in pine forests (Stephen and Browne, 2000). Synthetic formulations of entomopathogenic microorganisms, such as fungi, bacteria, and viruses, are being developed and evaluated. Efforts have

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focused on the fungus *Beauveria bassiana*, which under laboratory conditions has been demonstrated to cause high levels of mortality in several bark beetle species. However, most field experiments have produced less than satisfactory control (Barta et al., 2018). Tactics under development include contaminating beetles collected in traps and then releasing these individuals back into field populations to contaminate the pest population (Kreutz et al., 2010), and applying various suspensions of *B. bassiana* spores to the surfaces of felled and standing trees (Davis et al., 2018).

4.3.3 Sanitation

Sanitation, one of the oldest direct control tactics (Gmelin, 1787), involves identification of currently infested trees and subsequent felling and removal or treatment to destroy adults that could emerge from the tree and brood beneath the bark. Where it is economically feasible, trees may be harvested and transported to mills where broods will be killed during processing. Otherwise, felled trees are debarked, chipped, burned, or treated by solarization (i.e. placement of infested material in the direct sun). In the southeastern USA, a unique version of sanitation involves harvesting trees infested with southern pine beetle plus a buffer strip of uninfested trees to halt infestation (spot) growth (Swain and Remion, 1981). Research on sanitation focuses on combining sanitation with other direct control methods (e.g. semiochemicals) to increase reductions in levels of tree mortality attributed to bark beetles.

4.3.4 Insecticides

Hundreds of thousands of high-value trees in campground and urban areas may be treated with insecticides during bark beetle outbreaks in the United States, yet similar uses of insecticides are widely restricted in most European countries. Most treatments involve topical sprays of contact insecticides where it is important that all parts of the tree that are likely to be attacked are adequately protected (Fettig et al., 2013b). Recent advances in systemic insecticides have led to the development of injection systems that push adequate volumes of product (i.e. generally less than several hundred milliliters for even large trees) into the small vesicles of the sapwood (Grosman et al., 2010). Following injection, the product is transported throughout the tree to the phloem where bark beetles feed. Compared to topical sprays, tree injections represent essentially closed systems that eliminate drift and reduce non-target effects and applicator exposure, but proper timing of applications is critical to allow for full distribution of the active ingredient within the tree prior to the tree being challenged by bark beetles (Fettig et al., 2014a, 2017). Research focuses on gaining a better understanding of the timing required in different

systems (e.g. in high-elevation forests), and on combining systemic insecticides with fungicides to increase levels and duration of tree protection (Fettig et al., 2013b, 2014a).

4.3.5 Semiochemicals

The primary semiochemicals associated with the most aggressive bark beetle species have been isolated and identified, and combined with an integrated understanding of their context in the forest environment have led to several direct control methods (Seybold et al., 2018). For example, attractants such as aggregation pheromones and host kairomones are used to detect and monitor bark beetles, and to predict levels of tree mortality attributed to them. Attractants are also used in traps to collect and remove beetles from the forest (termed mass trapping), and placed on individual trees (termed trap trees) to induce attack prior to harvesting and sanitation. Repellents (inhibitors), such as the anti-aggregation pheromones verbenone and 3-methylcyclohex-2-en-l-one (MCH) and nonhost volatiles, are used to protect individual trees and forest stands (Zhang and Schlyter, 2004). Several formulations of anti-aggregation pheromones are commercially available (Seybold et al., 2018), and development of more effective blends (e.g. with nonhost volatiles) and formulations remains an important research focus (Fig. 3). In recent years, significant advances have also been made concerning the molecular biology and biochemistry of pheromone production in bark beetles, the synthesis of semiochemicals in the laboratory, the deployment of semiochemicals in the field, and the fate of semiochemicals once released into the active airspace of forests.

4.4 Indirect control

Numerous studies have demonstrated the effectiveness of reducing stand densities to increase resistance of trees to several bark beetle species (e.g. Wermelinger, 2004; Whitehead et al., 2006; Fettig et al., 2007, 2014b; but see Six et al., 2014). For example, Negrón et al. (2018) quantified the impacts of thinning implemented 2 years prior to a mountain pine beetle outbreak in the Black Hills, USA, and reported that the percentage of ponderosa pine (*P. ponderosa*) killed by mountain pine beetle during the outbreak was 34% in unthinned stands and 4% in thinned stands. In Europe, Heidger and Lieutier (2002) recommended thinning of spruce in order to reduce competition among trees, thereby increasing availability of water, nutrients, and sunlight allowing for enhanced growth and defense of residual trees against European spruce beetle. Thinning also has important influences on microclimate and tree spacing that affect resistance to bark beetles.

Figure 3 A relatively new bark beetle repellent for protection of individual conifers is SPLAT® Verb, a flowable and biodegradable formulation of the anti-aggregation pheromone verbenone that allows the user to adjust the size of each release point (dollop) in the field (Fettig et al., 2015). The inert ingredients are certified as food-safe by the US Environmental Protection Agency (EPA), and the product is classified as organic by the US Department of Agriculture. Other semiochemical-based tools for management of bark beetles with the SPLAT® matrix are under development. In this figure, multiple dollops of SPLAT® Verb have been applied to each aspect of the tree bole to study the effect of release rates on tree protection. Photo credit: R. Progar, Washington Office, USDA Forest Service.

For example, thinning may cause changes in wind speeds and direction within stands that cause turbulences that disrupt pheromone plumes used for recruiting conspecifics to the target tree during initial phases of host colonization (Thistle et al., 2004). This negatively affects host-finding success. Recent research indicates that thinning is effective for increasing

resistance to several bark beetle species even during 1000-year drought events (Negrón et al., 2009; Santos and Whitman, 2010; Fettig et al., 2019; Restaino et al., 2019). However, given projected increases in drought stress (Vose et al., 2018), tree-density (stocking) thresholds are being reevaluated and lowered to maintain adequate levels of resistance to bark beetles during severe droughts (e.g. in the southwestern United States). Prescribed fire may also be used to manage stand densities in some forests, and while short-term (e.g. 1–5 years) increases in bark beetle–caused tree mortality are likely (due to stress induced by sublethal heating of plant tissues) in the longer term burned areas benefit from the positive impacts of prescribed fire on growing space (Fettig and McKelvey, 2014).

5 Advances in defoliator monitoring and management

The majority of defoliator pest species of boreal and temperate forests are within the order Lepidoptera (Table 2). Population regulation of defoliators occurs naturally *via* bottom-up (host tree defense) and top-down (natural enemy) controls. At low-to-moderate levels of defoliation, tree growth may decline, but most trees survive. During population outbreaks, large-scale tree mortality can occur following cumulative defoliation over several years. Protecting forests from outbreaks of defoliators is a complex, expensive, and often controversial process, especially when it involves harvesting of trees and aerial spraying of insecticides. Aerial application of insecticides began in the late nineteenth century, but due to increasing environmental concerns has been largely replaced by biological control.

5.1 Direct control

5.1.1 Microbial biological control

Microbial biological control, which includes entomopathogens such as viruses, bacteria, and fungi, are commonly used in management of forest defoliators (see Sections 7.3 and 7.5). In North America, the *Lymantria dispar* nucleopolyhedrosis virus (LdNPV) is the most documented factor causing the collapse of European gypsy moth populations (McManus and Csoka, 2007; Hajek and van Nouhuys, 2016). With modern molecular technology, complete genome sequences are known for several forest insect viruses including NPV associated with several budworm species (*Choristoneura* spp.), white marked tussock moth (*Orgyia leucostigma),* European gypsy moth (Harrison et al., 2016), and sawflies (*Neodiprion* spp.) (van Frankenhuyzen et al., 2016). Application of sequence homologies has allowed a specific insect species to be targeted, and thereby facilitated approval of viruses in control strategies used by regulatory agencies (Lapointe et al., 2012).

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The first commercial product of a bacterium, *Bacillus thuringiensis,* was produced in California in 1957. Now commonly known as Bt, the strain *B. thuringiensis* var. *kurstaki* (*Btk*) has since been used as an alternative for chemical insecticides in large-scale aerial spray operations to control multiple defoliator species (van Frankenhuyzen et al., 2016; Fuentealba et al., 2019). A ubiquitous microsporidian pathogen of spruce budworm, *Nosema fumiferanae*, was evaluated for microbial control in field trials during a spruce budworm outbreak in eastern Canada in the 1970s. However, recent studies indicate that it may act in concert with other density-dependent factors, and that direct mortality due to this pathogen is limited (Eveleigh et al., 2012). The use of molecular techniques will increasingly facilitate the development of novel microbial-based pest management options.

5.1.2 Natural enemy (insect) biologica control

Defoliator outbreaks occur when control by natural enemies becomes ineffective, allowing relatively uncontrolled population growth. Natural control of forest defoliators occurs largely by parasitoids (Nealis, 1991), primarily wasps and flies that deposit eggs on, in, or near specific immature life stages of the defoliator (i.e. eggs, larvae, or pupae). Parasitoid larvae later hatch and consume the defoliator host. Classical biological control takes advantage of the role of natural enemies, including parasitoids, in regulating population growth. Biological control of defoliators has been implemented for at least a century, with varying success (MacQuarrie et al., 2016; Kenis et al., 2017), by rearing and releasing natural enemies into outbreak areas. Most biological control programs in Europe and North America have targeted non-native pest species by introducing a non-native biocontrol agent from the native range of the non-native pest. In Europe, around 750 parasitoids and predators have been introduced against lepidopteran pests of woody plants since 1870, of which only 2% are considered successful (Kenis et al., 2017). In North America, introduced and established parasitoids of European gypsy moth can cause significant mortality of larvae and pupae (McManus and Csoka, 2007; Fuester et al., 2014).

In many defoliator species, regulation by natural enemies determines outbreak intensity and duration. For example, specialist parasitoids can have a rapid numerical response and increased capacity to control outbreak populations of the forest tent caterpillar (*Malacosoma disstria*) and hemlock looper (*Lambdina fiscellaria*), resulting in frequent outbreaks of short duration (Hébert et al., 2001; Roland, 2005). In contrast, the parasitoid community affecting the spruce budworm is dominated by generalist species whose slow numerical response (Eveleigh et al., 2007) creates outbreak cycles of relatively longer period and duration (Régnière and Nealis, 2007). The abundance and

efficacy of parasitoids varies with landscape structure (Roland and Taylor, 1997), and increased forest diversity has been associated with slower expansion rates of spruce budworm outbreaks and lower outbreak intensity (Robert et al., 2018). Forest fragmentation and losses in diversity can therefore influence outbreak duration and spread of defoliators through effects on their natural enemies (Roland, 1993).

5.1.3 Semiochemicals

The use of semiochemicals for management of defoliators includes pheromones to attract mates or conspecifics and kairomones (i.e. plant volatile cues) (Evenden and Silk, 2016). The most common uses of sex pheromones are for detection, monitoring (Schmidt et al., 2003), population suppression (reducing populations to mitigate damage from defoliation), implementing barrier zones to slow spread from infested areas (e.g. for gypsy moth 'Slow The Spread' (STS), see Section 7.5.2), and eradication of isolated infestations in uninfested areas. Mass trapping uses pheromones to attract insects to traps where the pests are then killed with an insecticide. Mating disruption reduces mating success by disorienting males through saturation of the environment with pheromone (Witzgall et al., 2010). (+)-Disparlure attracts male European gypsy moths, and baited 'delta traps' have been deployed in western Canada in a grid across landscapes to detect and eradicate moth populations that have been repeatedly intercepted but not successfully established (Nealis, 2009). 'Disrupt Micro-flake spruce budworm' (Hercon Environmental, Emigsville, Pennsylvania, USA) was aerially applied to stands infested by spruce budworm in Canada where it reduced mate-finding by males, but there was no decrease in the number of egg masses laid (Rhainds et al., 2012; Evenden and Silk, 2016). Dispersal of female moths into treated areas is thought to limit the effectiveness of mating disruption in the spruce budworm. In contrast, mating disruption with sex-attractant pheromones has been a key component of the European gypsy moth STS program in the United States (Onufrieva et al., 2019) (Section 7.5.2). These differences highlight how targeting isolated populations with mating disruption can result in greater efficacy than when targeting widely established outbreak populations.

5.2 Indirect control

Bottom-up control of defoliators can be accomplished by creating healthy, vigorous forest stands *via* silvicultural practices. Stressed trees in forest plantations are susceptible to defoliators and can facilitate buildup of populations that can trigger a larger outbreak (Björkman et al., 2015; Muzika, 2017).

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Maintaining high tree species diversity can decrease buildup of specialist defoliator populations by conferring 'associational resistance' to host species of the pest when it occurs among nonhosts (Jactel et al., 2017). There is evidence that pre-commercial thinning to increase black spruce proportions in mixed fir-spruce stands, or increasing hardwood content in the landscape could reduce overall tree mortality during spruce budworm outbreaks (Campbell et al., 2008; Pothier et al., 2012). Fragmenting the forest landscape by planting nonhost tree species can disrupt host-finding behavior of ovipositing females by making suitable hosts relatively less apparent. In generalist defoliators, however, the response to tree diversity can be variable (Moreira et al., 2016). Tree species diversity can also increase the diversity and abundance of generalist parasitoids that would serve as natural controls and potentially decrease population growth rates (Roland and Taylor, 1997). Maintaining stand age diversity would also decrease density of mature trees that may be susceptible to defoliation. Finally, removal of susceptible trees by logging and infested branches by pruning in the wake of an outbreak can mitigate the impacts of defoliation. Low population densities of tent caterpillars (*Malacosoma* spp.) in North America and processionary moths (*Thaumetopoea* spp.) in Europe and North Africa can be controlled by mechanically removing larval colonies (Ciesla, 2011).

6 Advances in invasive species monitoring and management

Non-native invasive forest insects have threatened and damaged trees in northern boreal and temperate forests for over 150 years (Liebhold et al., 1995; Niemelä and Mattson, 1996), and, more recently, they have become a major focus of forest insect management (Langor et al., 2009; Aukema et al., 2010; Liebhold et al., 2017). Native invasive species that have been moved or have dispersed into new ecological contexts within the geographical borders of countries have also been vexing, both biologically and politically (Table 3, e.g. Baranchikov et al., 2010; Seybold et al., 2019). Many of these invasive species have had only minor, localized, or regional impacts on forest or shade trees, but some have become major pests with landscape-level impact (Table 3, Tobin and Liebhold, 2011; Herms and McCullough, 2014). In an assessment of more than 450 invasive forest insect species that have established populations in the United States, Aukema et al. (2010) considered 14% (62 species) as 'high impact' species, that is, of regulatory significance or having caused notable damage to forests or urban forest trees. The US Department of Agriculture (USDA) Forest Service has also recently completed a comprehensive assessment of invasive species with a focus on those organisms that interact with forest and rangeland ecosystems (Poland et al., 2019). The assessment covers the full range of issues from risk assessment, monitoring/detection, impact, and management to economics and sociological issues. It also provides summaries that highlight

invasive species of concern by US region. In this section, we will focus on the most recent advances in detection, monitoring, and management of invasive forest insect species.

6.1 Detection and monitoring

Traditionally, the detection of invasive forest insects was a matter of chance encounters through hand collection or observation of sudden and surprising tree damage patterns (Coleman and Seybold, 2008). Taxonomic specialists kept records and maintained primary awareness of native and adventive distributions of potential pest taxa (Wood and Bright, 1992). More recently, systematic approaches to detection have emerged by targeting ports of entry, urban parks and arboreta, green waste facilities, agricultural habitats, and similar areas through inspection and trapping with generic and specific semiochemical lures (Seybold et al., 2016; Rabaglia et al., 2019). There is also growing recognition that trees in urban and agricultural habitats can provide landscape-level bridging for forest pests into forest habitats (Rossi et al., 2016). Diverse collections of plants organized into geographically dispersed and formalized networks can also provide powerful opportunities for early detection of invading insects that impact trees (Barham, 2016). The invasion process has been preempted still further by focusing on 'overseas' surveillance where, for example, United States and Canadian forest entomologists have long pursued a cooperative assistance program with their foreign counterparts in and around ports of entry in the Russian Far East, Japan, Korea, and China to detect and manage potential lepidopteran invaders (USDA, 1993; Humble et al., 2013; Freyman, 2015; USDA APHIS, 2016). Recently, this concept has been extended to Asian-sourced ambrosia beetles and their pathogenic fungi, which have emerged in the early twenty-first century as preeminent invasive pests of trees (Hulcr and Dunn, 2011; Hulcr et al., 2017). The development of molecular techniques based on multiple genes or even full genomes has facilitated confirmatory identifications of species, subspecies, strains, and biotypes to provide an informative end point to the detection process (EPPO, 2016; Thomas et al., 2016; Bilodeau et al., 2019; Roe et al., 2019).

Risk assessment and pathway analysis have also received greater attention in the planning and allocation of limited resources to address invasive species monitoring and detection (Venette et al., 2010; Fuentealba et al., 2013; Susaeta et al., 2016; Hudgins et al., 2017). For example, Gray (2017) described an analysis of the risk of the invasion pathway of the Asian gypsy moth (*Lymantria dispar asiatica*) into North America through an evaluation of its 'stowaway' pathway on containers or cargo on ships from regulated (Asian) ports to protected (North American) ports. The analysis involved the consideration of the propagule

size on ships; the probability of propagule release in the protected port; and the survival and establishment of propagules in that port. In this instance, the propagules are newly hatched larvae. A gypsy moth phenology model specific for the location of the protected port was useful for providing the pathway specifics for the three criteria.

6.2 Management

Management strategies for invasive forest insects rely on tactics described in the earlier sections on bark beetles (Section 4) and defoliators (Section 5) with the addition of the potential for preventing arrival of incipient populations through rigorous quarantine and inspection programs, as well as local or complete eradication of nascent populations. When prevention or eradication of an invading population is not possible, retarding the spread rate throughout the new range may have economic and ecological benefits (see Section 7.1.2: SLow Ash Mortality (SLAM) for the invasive emerald ash borer and 7.5.2: Slow The Spread (STS) for the European gypsy moth as two North American examples). Generally, extensive efforts have been made to carry out classical biological control programs to exert some level of natural population regulation of an invasive forest insect (e.g. Duan et al., 2014). Similarly, cultural practices involving re-planting with resistant cultivars of host species or closely related species have been investigated and attempted (Rebek et al., 2008; Villari et al., 2016) (see Section 3). After establishing the impact of an invasive forest insect species on the adventive forest resources (Muzika and Liebhold, 1999; Eyles et al., 2011; Coleman et al., 2012), there has been increasing attention and effort to apply silvicultural methods to manage well-established populations of invasive species (Dodds et al., 2014; Muzika, 2017). Thus, the full range of integrated pest management techniques can in theory be applied to invasive forest insects once they have become established in a new habitat.

7 Case studies

7.1 Emerald ash borer

Since its discovery in southeastern Michigan, USA, in 2002, the emerald ash borer (see Table 3) has killed hundreds of millions of ash trees with devastating economic and ecological impacts and threatens the entire North American ash resource (Poland and McCullough, 2006; Gandhi and Herms, 2010; Kovacs et al., 2010; Flower et al., 2013; EAB Info, 2019). Early efforts to eradicate isolated infestations were unsuccessful; therefore, considerable research has been conducted to develop effective detection and management tools in North America.

7.1.1 Early detection, monitoring, and management

Early detection of low-density infestations is notoriously difficult because of emerald ash borer's cryptic oviposition and feeding behavior under the bark and lack of external signs or symptoms until trees are severely damaged and adults have emerged (Poland and McCullough, 2006). Adults are attracted to stressed or girdled ash trees (McCullough et al., 2009a,b), leaf and bark volatiles including *cis*-3-hexenol (de Groot et al., 2008) and sesquiterpenes found in Manuka oil (Crook et al., 2008), and shades of green or purple color (Francese et al., 2010a). A female-produced pheromone, *cis*-lactone (a macrolide), may also enhance close range attraction (Ryall et al., 2012). The most promising trap designs for early detection of emerald ash borer include green funnel traps (Francese et al., 2011), green or purple sticky prism traps hung in the ash canopy (Francese et al., 2010b), or green or purple double-decker traps (Poland et al., 2011; Poland and McCullough, 2014). Early identification of infestations with traps allows for rapid implementation of management tactics.

Current management strategies for emerald ash borer in North America have shifted toward integrated area-wide programs designed to reduce population growth in infested areas and slow its spread to non-infested areas. Integrated management programs include public outreach (Mercader et al., 2013); surveys by using artificial traps and girdled trap trees; quarantines and other regulatory activities that reduce risk of human transport of emerald ash borer-infested materials (USDA APHIS, 2019); removal and destruction of infested trees (McCullough et al., 2015; Mercader et al., 2015, 2016); application of systemic insecticides to protect trees (Smitley et al., 2010; McCullough et al., 2011); and release of natural enemies for biological control (Duan et al., 2014; Bauer et al., 2015; Jennings et al., 2016).

Insecticide treatments, such as trunk injection of systemic insecticides (emamectin benzoate, azadirachtin), basal trunk sprays (dinotefuran), or soil applications (imidacloprid, dinotefuran), are effective at protecting high-value landscape trees in urban areas (McKenzie et al., 2010; Smitley et al., 2010; McCullough et al., 2011), although costs and environmental concerns prevent widespread use in forested areas. Therefore, biological control is being evaluated for long-term sustained management of emerald ash borer in natural forests (Bauer et al., 2015). Two of three introduced Asian parasitoids (*Tetrastichus planipennisi* and *Oobius agrili*) have established stable populations in several US states (Duan et al., 2018). These species, along with some native natural enemies, have substantially reduced emerald ash borer population growth in some locations (Duan et al., 2014). A fourth parasitoid native to Russia (*Spathius galinae*) was approved for release in 2015 (USDA APHIS, 2015). Research is also being conducted to develop hosts that are resistant to emerald ash borer for use in restoration of heavily impacted ecosystems (Koch et al., 2015; see Section 3).

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7.1.2 SLow Ash Mortality (SLAM)

Multiple agencies in the United States including the USDA Forest Service, USDA APHIS, Michigan Department of Natural Resources, Michigan Department of Agriculture and Rural Development, Michigan State University, and Michigan Technological University partnered to conduct a large pilot study to evaluate the SLAM integrated strategy for managing the emerald ash borer (Poland and McCullough, 2010; McCullough and Mercader, 2012). Though a very small proportion of ash trees in the >390 km^2 project area were treated with insecticides or girdled, both tactics reduced emerald ash borer densities and protected ash trees in areas surrounding the treatments (Mercader et al., 2015). Recently, area-wide management approaches integrating biological control and selective use of insecticides have been initiated. Integrating these components may yield additive or synergistic effects (McCullough and Mercader, 2012) as insecticides impact newly hatched neonate larvae and adults that both feed on leaves (Smitley et al., 2010; McCullough et al., 2011), whereas natural enemies parasitize eggs or later-instar larvae (Bauer et al., 2015). Landscape-level integrated management strategies such as SLAM and biological control, insecticide treatments in urban areas, collection and preservation of ash seed, and development of more resistant ash (Section 3) offer hope for the protection of ash and persistence of the genus at some level in urban environments and forests of North America.

7.2 Mountain pine beetle

Mountain pine beetle is the most significant forest insect pest in North America, and colonizes multiple pine species (Negrón and Fettig, 2014; Table 1). The geographic distribution generally reflects the range of its primary hosts, although lodgepole pine extends further to the north in Canada and ponderosa pine and other pines extend further to the south in Mexico than where mountain pine beetle populations currently exist (Bentz et al., 2019). Since 2000, ~10.3 million ha have been impacted by mountain pine beetle in the United States alone (Berner et al., 2017), which represents almost half of the total area impacted by all bark beetles species combined in the western United States during this period.

Historically, the range of mountain pine beetle was restricted by climatic conditions unfavorable to brood development and survival, despite the availability of host trees, but the pest distribution is expanding northward due to climate change (Table 5) and other factors including lower defenses in novel hosts (Erbilgin, 2019). By the end of the twenty-first century, thermal suitability for mountain pine beetle population success is projected to be high at the most northern extent of pines in Canada, although portions of the historical range are projected to become unsuitable due to excessive warming that disrupts overwintering and adult emergence timing (Bentz et al., 2010, 2019). Models

also project that thermal suitability for mountain pine beetle in pine forests further south of the current range, including Mexico and the southwestern United States, will increase throughout the century. Mountain pine beetle is the second most intensively studied bark beetle after European spruce beetle (see Section 7.4). A century of research has produced thousands of scientific papers and a wealth of knowledge applicable to the management of this species (Table 6), much of which is captured in several syntheses (e.g. Berryman et al., 1978; Safranyik and Wilson, 2006; Negrón and Fettig, 2014). Researchers continue to develop valuable knowledge and tools, of which we highlight a few of many recent examples below.

7.2.1 Fuels and fire behavior

During the previous decade, substantial research on the effects of mountain pine beetle outbreaks on forest fuels and surface and crown fire behaviors has revealed that mountain pine beetle and wildfires are principal drivers of change in western North American forests. Much of the knowledge generated has been synthesized by Jenkins et al. (2008, 2014), Hicke et al. (2012), and Kane et al. (2017). Practical implications relevant to firefighter safety are discussed in Jenkins et al. (2012, 2014).

Immediately following tree colonization, changes occur in needle moisture content and chemistry that influence flammability (Page et al., 2012). As time progresses (years to decades following an outbreak), significant increases occur in the accumulations of large coarse woody surface fuels (100- and 1000-hr fuels) (Jenkins et al., 2014). As such, several attempts have been made to predict fire behavior in mountain pine beetle–affected stands by using existing fire behavior models. Generally, predicted surface fire rates of spread and fire line intensities are higher during (e.g. initial 1–5 years) and then again decades after an outbreak. The literature is more mixed concerning outbreak effects on crown fire behavior, and confounded by the heterogeneity of crown fuels in beetle-impacted forests that violates the fundamental assumptions of homogeneity in the application of fire behavior models (Cruz and Alexander, 2010). Regional-scale studies have reported negligible effects on fire severity and scale (e.g. Hart et al., 2015; Meigs et al., 2015), especially under extreme fire weather conditions. Differences in the severity and distribution of outbreaks, time since outbreak (i.e. the 'bark beetle rotation'; Jenkins et al., 2008), dominant fire regime, and the retrospective nature of most studies challenge our understanding of these relationships.

7.2.2 Semiochemical-based tools

Research concerning semiochemical-based tools and tactics for mountain pine beetle has progressed steadily since the late 1960s, resulting in tactics

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Table 6 Monitoring and management tools for mountain pine beetle

Detection and survey	Many methods are available, but aerial detection surveys using trained observers with digital sketch-mapping equipment remains most relevant (Fig. 2). Recent advances have been made with remotely sensed data from satellites, but there are limitations to their applicability (Wulder et al., 2012).
Risk and hazard rating systems	Several risk and hazard rating systems are available. The most relevant is that of Shore and Safranyik (1992) for use in lodgepole pine. Susceptibility is calculated based on four factors: (1) percentage of susceptible basal area (trees ≥15 cm dbh); (2) average stand age of dominant and co-dominant trees; (3) stand density of all trees ≥7.5 cm dbh; and (4) the geographic location of the stand in terms of latitude, longitude, and elevation. The proximity and size of local mountain pine beetle populations are added to compute an overall index. Several systems are available for use in other host types (Fettig et al., 2014c).
Insecticides	The use of insecticides for tree protection involves topical sprays and systemic insecticides injected directly into the tree (Fettig et al., 2013b). Remedial applications to kill adults and brood within currently infested hosts are no longer used.
Semiochemicals	The use of semiochemicals includes applications of aggregation pheromones and co-attractants (e.g. host volatiles) for survey and detection and trap-out, trap-tree, or push-pull tactics; and applications of repellents (inhibitors) for protection of individual trees and forest stands (Progar et al., 2014; Seybold et al., 2018). Verbenone is the most widely used repellent semiochemical.
Sanitation	In some cases, emphasis is placed on removal of newly infested trees to reduce the quantity of attractive semiochemicals (i.e. aggregation pheromones and host volatiles) released into the forest stand, but this is rare due to complications regarding the identification of newly attacked trees and the level of responsiveness required in their removal. Sanitation combined with the use of verbenone is recommended for mitigating small infestations in lodgepole pine forests (Progar et al., 2014).
Thinning	Thinning has long been advocated as a preventive measure. Common tactics include thinning from above or diameter-limit thinning; thinning from below; removal of trees with thick phloem; and increasing residual tree spacing (Fettig et al., 2014c). Thinning is likely most effective when implemented several years (to decades) prior to an infestation, and when appropriate stand densities are maintained over time (but see Negrón et al., 2018).
Increasing landscape heterogeneity	Increasing heterogeneity (e.g. of age, size, and tree species compositions) increases resistance of forested landscapes to mountain pine beetle (Fettig et al., 2014c).
Reducing the rate of atmospheric warming	Forests are increasingly vulnerable to mountain pine beetle as a result of the direct and indirect effects of climate change (Bentz et al., 2019).

for monitoring and detection, and for reducing levels of tree mortality at various spatial scales. Much of this work has been synthesized by Progar et al. (2014) and Seybold et al. (2018). Recent advances include development

and commercialization of verbenone-releasing flakes for aerial treatment of large (e.g. >100 ha) areas (Gillette et al., 2009, 2012), and of a flowable and biodegradable formulation that is hand applied (SPLAT® Verb; Fettig et al., 2015b) (Fig. 3). After researchers demonstrated that combinations of green leaf volatiles and angiosperm bark volatiles could disrupt attraction of mountain pine beetle to baited trees (see Seybold et al., 2018), nonhost volatiles became the focus of numerous studies in hopes of increasing levels of tree protection over those from application of verbenone alone. Perhaps most notable, Fettig et al. (2012a,b) developed Verbenone Plus [acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and (–)-verbenone], which has been demonstrated to be effective for tree protection in several studies in western Canada and the western United States, but has not yet been commercialized. An obstruction to the use of semiochemical-based tools for tree protection is the high cost of production, but recent advances in synthesis have lowered costs (Chou and Keasling, 2012).

7.2.3 Insecticides

Fettig et al. (2013b) discuss the efficacy, residual activity, and environmental safety of insecticides used to protect high-value trees near homes and in campgrounds from mountain pine beetle attack. Recent advances include the development and commercialization of several contact insecticides and alternative timings of associated treatments (Fettig et al., 2006a,b, 2015a, 2018), and of systemic insecticides applied through tree injection systems (Grosman et al., 2010; Fettig et al., 2014a,b). Other research has focused on the environmental fate of insecticides resulting from conventional spray applications, where the amount of drift that occurs was found to pose little threat to adjacent aquatic environments (Fettig et al., 2013b).

7.3 Spruce budworm

Regional outbreaks of spruce budworm (Table 2) have occurred about every 35 years in Canada and the northeastern United States on balsam fir (*Abies balsamea*) and spruce, leading to development of integrated management strategies. Planting of nonhosts, including pines, rather than host species and increasing the proportion of hardwoods on the landscape can reduce population buildup (Campbell et al., 2008; Pothier et al., 2012).

7.3.1 Spruce Budworm Decision Support System

The Spruce Budworm Decision Support System (SBWDSS) relies on forest inventory, stand yield, and growth models, as well as harvest scheduling

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information to estimate losses in timber supply and to facilitate forest management operations (MacLean et al., 2002). In addition to preventive silviculture operations (Pothier et al., 2012), mature, high-value stands are sprayed with biological control products (see Section 5.1) above the canopy with aircraft. The most frequently used is *Btk* (see Section 5.1.1), a microbial insecticide that causes mortality by rupturing the midgut of feeding larvae, quickly halting feeding, and protecting trees from further defoliation (Fuentealba et al., 2019).

7.3.2 Early intervention strategy

Following the last outbreak of spruce budworm in eastern Canada (ca. 1960–1992) that resulted in losses of 382 million m^3 of timber between 1977 and 1987 alone (Sterner and Davidson, 1982), the implementation of an "early intervention strategy" is being tested during a current outbreak that began in Quebec, Canada, in 2006. Spruce budworm is a highly mobile species, and control actions aim to suppress populations prior to large-scale defoliation events, and early enough to prevent moth dispersal into neighboring uninfested forests. The early intervention strategy is based on principles of population dynamics and Allee effects that can diminish population growth rates. Allee effects cause a decline in per capita population growth when population density decreases below a critical threshold and can limit establishment when sufficient mates are not available (Liebhold and Tobin, 2008). At low population densities, spruce budworm is subjected to strong predator-driven and mate-finding Allee effects (Régnière et al., 2013). Unless populations are subsidized adequately by eggs from immigrating moths, decreasing growth rates occur. A main goal of the early intervention strategy is to reduce the density of newly detected outbreak spots below thresholds for mating success. Several products are used to accomplish this including *Btk* and aerial application of an insect growth regulator tebufenozide (Mimic®) and a pheromone-based mating disruptant (Disrupt Micro-Flake SBW®). Current tests began in 2014 in New Brunswick, which is geographically a potential sink for dispersing moths from the outbreak in Quebec.

Current research focuses on evaluating the ability of treatments to (1) reduce spruce budworm populations to levels below Allee thresholds where negative density-dependence occurs, (2) evaluate the rate at which immigrating moths re-invade areas where populations have been suppressed, and (3) evaluate the long-term response of natural enemies to the suppressed spruce budworm population (SBW EIS Phase 2 Project Proposal 2017). Early results demonstrate that spruce budworm populations in treated "hot-spots" have lower larval survival rates compared to control stands (Martel et al., 2018). If successfully implemented, this strategy,

which integrates basic science with applied science as well as emerging technologies, can mitigate timber losses and the need for costly control measures during an outbreak.

7.4 European spruce beetle

The European spruce beetle is the most important forest insect in Europe, and colonizes predominantly Norway spruce (Table 1). Outbreaks are often incited by other disturbances, such as windstorms, which provide an abundance of weakened host material that fosters rapid increases in population densities (Marini et al., 2017). Due to vast forest exploitations in the past and current wood demands, Norway spruce is now widely distributed outside its native range (Kölling et al., 2009), and is frequently found on unsuitable sites in Central Europe where it is highly susceptible to European spruce beetle.

In the last three decades across eight European countries, the amount of timber damaged by European spruce beetle outbreaks was driven by increasing summer rainfall deficit (drought), warm temperatures, and the density of storm-felled trees from the previous year (Marini et al., 2017). Warming temperatures are increasing the area of spruce habitat that supports two rather than one generation per year (Netherer et al., 2015) and a higher number of sister broods (Davídková and Doležal, 2017), both of which can benefit population growth. Models have been developed to predict how changing temperatures will influence these traits (Baier et al., 2007; Jönsson et al., 2009, 2011; Siedl and Rammer, 2017) (Table 5; Section 2.1). In one case study, model projections suggest that these trends will continue throughout the twenty-first century with an ~30% increase in European *Picea* habitat supporting a second generation (Bentz et al., 2019). Model results also project high thermal suitability for European spruce beetle population growth in potentially invadable *Picea* habitat in North America throughout this century, highlighting the importance of continued monitoring at North American ports (see Section 6.1).

Several centuries of research have produced thousands of scientific papers and a wealth of knowledge applicable to the management of European spruce beetle (Table 7), much of which has most recently been synthesized by Wermelinger (2004) and Fettig and Hilszczański (2015). Since publication of the first forestry text that addressed bark beetles (Ratzeburg, 1839), control methods have been developed systematically and employed regularly to reduce tree losses attributable to this species. During outbreaks, thousands of trees are attacked and killed within weeks prompting large and well-coordinated management efforts by several countries (e.g., Table 8). Researchers continue to develop valuable knowledge and tools, of which we highlight a few of many recent examples below.

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7.4.1 Biocontrol

To date, biological control has not been formally implemented for European spruce beetle. However, some recent efforts concerning development of *B. bassiana* are considered to be promising. Research focuses on improving the virulence of formulations under field conditions, and on developing effective methods of delivery of *B. bassiana* into wild populations of European spruce beetle (Kreutz et al., 2010; Barta et al., 2018). Patents have been procured for a low-molecular polyethylene matrix that stabilizes *B. bassiana* spores and conidia, and for a trap that serves as an autoinoculation device for captured individuals.

7.4.2 Semiochemical-based tools

Research concerning semiochemical-based tools and tactics for management of European spruce beetle has progressed steadily since the 1970s, but despite this, they are largely limited to the use of attractants for survey and detection, mass trapping (trap-out), and trap-tree methods. This is somewhat of an artifact of the effectiveness and prevalence of sanitation for control of European spruce beetle throughout most of Europe (Tables 7 and 8). In recent decades, the development of behavioral repellents (inhibitors) has received some attention (Zhang and Schlyter, 2004); however, the most active blends contain several components in addition to verbenone (e.g., Schiebe et al., 2011), which are too costly for widespread use. As such, recent research has focused on refining these blends and reducing the number and cost of components required to impart tree protection. Unelius et al. (2014) reported that a blend consisting of verbenone, 1-hexanol, and *trans*-conophthorin is a cost-efficient repellent warranting more widespread use where sanitation is not feasible. In Germany, related research focuses on developing strategies that apply SPLAT® Verb to prevent the buildup of high population densities after disturbances such as windstorms.

7.5 European and Asian gypsy moths

Larvae of gypsy moths and related species (e.g., nun moth, pink gypsy moth, *L. mathura*, and other Asian species such as *L. albescens*, *L. postalba,* and *L. umbrosa*) are noted defoliators of forest trees (Tables 2, 3, and 5; Pogue and Schaefer, 2007; Tobin and Liebhold, 2011). The European gypsy moth, primarily a hardwood defoliator, was introduced and established in the eastern portion of the United States in the late 1860s (Liebhold et al., 1989). The Asian gypsy moth originates from temperate Asia (i.e., north of the Himalayas) ranging from the Ural Mountains east to China, Korea, the Russian Far East, and Japan, and there have been frequent introductions and attempted eradications of this

Table 7 Monitoring and management tools for European spruce beetle

Risk and hazard rating systems	Several attempts to develop risk and hazard rating systems have been made or are being developed (e.g., Netherer; Nopp-Mayr, 2005, Kautz et al., 2018). More sophisticated models, such as PHENIPS, provide a tool for hazard rating at local and regional scales (Baier et al., 2007).
Detection and survey	Infested trees are located *via* ground surveys executed by well-trained technicians. Initial attempts using unmanned aerial vehicles for survey and detection have failed (Ackermann et al., 2018). Johansson et al. (2019) suggest that dogs are able to detect infested spruce from the first hour of bark beetle attack until several weeks after attack, and are more efficient than humans in detecting early infestations.
Sanitation	By far, sanitation is the most frequent and effective direct control method for European spruce beetle. In many countries, infested trees are located by systematic searching on foot and marked for removal by trained technicians fully employed throughout most of the year. Trees recently damaged by windstorms or other disturbances are also often salvaged at this time (Göthlin et al., 2000).
Insecticides	The use of insecticides for management of European spruce beetle is highly restricted in most countries. During sanitation, insecticides may be used to treat infested logs stored along forest roads if they cannot be removed prior to beetle emergence.
Semiochemicals	The use of semiochemicals includes applications of aggregation pheromones and co-attractants (e.g., host volatiles) for survey and detection, mass trapping (trap-out), and trap-tree methods. Repellents (inhibitors) are not widely used (Fettig and Hilszczański, 2015).
Trap trees	Damaged and windthrown trees are often used as trap trees. Trees may be baited with synthetic pheromones and are several times more effective at trapping European spruce beetle than pheromone-baited traps (Raty et al., 1995).
Thinning	Thinning has long been advocated as a preventive measure (Wermelinger, 2004).
Increasing landscape heterogeneity	Increasing heterogeneity (e.g., of age, size, and tree species compositions) and diversity increases resistance of forested landscapes (Wermelinger, 2004).
Reducing the rate of atmospheric warming	Forests are increasingly vulnerable to European spruce beetle as a result of the direct and indirect effects of climate change (Marini et al., 2017).

subspecies near shipping ports of entry in western North America (Myers et al., 2000; Gray, 2017). These ecologically and behaviorally distinct subspecies were at first distinguished by mitochondrial and nuclear DNA sequencing techniques, including microsatellite DNA analysis (Bogdanowicz et al., 1997, 2000), but have been analyzed more recently with increasingly sophisticated approaches and methodologies (Islam et al., 2015; Stewart et al., 2016; Djoumad et al., 2017). With its broader host range (that includes conifers) and the flight capacity of females, Asian gyspy moth is considered a greater threat

Table 8 Methods of control for European spruce beetle during outbreaks in southern Poland, 2007–2010

Method	2007	2008	2009	2010	Total
Trap trees (thousands)	8.4	5.2	4.4	3.7	21.7
Baited-trap trees (thousands of trees, m^3)	17.5	30.9	31.7	16.2	96.3
Marked (infested) trees (thousands)	510	424	272	158	1364
Sanitation (thousands of trees, m^3)	803	798	466	231	2298
Debarked-infested trees (thousands of trees, m^3)	297	254	17	23	591
Pheromone-baited traps (thousands)	11.6	12.2	11.8	10.6	46.2

Source: based on Szabla (2013); adapted from Fettig and Hilszczański (2015).

to the forests of western North America and elsewhere outside of its native range (Peterson et al., 2007). Both subspecies continue to be detected in a network of sex pheromone–baited traps in North America (Tobin and Liebhold, 2011; CFPC, 2010–2017).

7.5.1 Advances in population biology

The long-established populations of European gypsy moth in eastern North America have provided opportunities for research on an invasive hardwood defoliator with periodic outbreak potential (Liebhold et al., 2007; Liebhold and Tobin, 2008; Grayson and Johnson, 2018). The original introduced population has spread steadily from Massachusetts, USA, to include most of the northeastern United States, as well as portions of the midwestern and southeastern United States. The areas of research coupled with this invasion have included local establishment and spread of populations, dynamics, and regulation of populations, impacts of populations, and multiple aspects of management (Table 9).

7.5.2 Management by slowing the rate of population spread

Managing populations of European gypsy moth in North America has involved three approaches: suppression of outbreak populations within the generally infested area; eradication of satellite populations detected at great distance from the generally infested area (typically in the western United States or Canada); and attenuating the spread of populations from the generally infested area. The latter approach, "Slow the Spread" (STS) is a US state-federal cooperative program, whose objective is to retard the spread of European gypsy moth into new areas (Leuschner et al., 1996; Sharov et al., 1998, 2002b; Tobin et al., 2004; McManus, 2007). Several regional integrated pest management programs targeting gypsy moth were the progenitors for STS, which debuted on a small

Table 9 Research advances in the population biology and management of European gypsy moth in North America

Establishment and spread of populations	Fundamental research on the establishment and spread of invasive populations has provided the basis for management of the range expansion of *L. d. dispar* in North America (Sharov et al., 1996b, 1998; Sharov and Liebhold, 1998; Johnson et al., 2006; Liebhold and Tobin, 2006; Liebhold et al., 2007; Tobin et al., 2015; Streifel et al., 2017).
Dynamics and regulation of populations	Low-density populations of *L. d. dispar* appear to be loosely regulated in an inversely density-dependent manner through predation by small mammals; one of the largest sources of mortality in most *L. d. dispar* populations is the fungal pathogen *Entomophaga maimaiga*, which acts largely in a density-independent fashion (Elkinton and Liebhold, 1990; Liebhold, 1992; Liebhold et al., 2000; Tobin and Hajek, 2012; A.M. Liebhold, personal correspondence).
Impact	Partial or total defoliation of oak canopies by *L. d. dispar* often result in tree growth loss, severe physiological stress, and, when exerted over consecutive years or with other sources of stress, tree death. Greatest economic impacts occur in residential areas, where loss of foliage and occasional tree mortality are compounded by the considerable nuisance of large quantities of caterpillars and their urticating hairs and frass (Muzika and Liebhold, 1999, 2000; Morin et al., 2004; Tobin and Liebhold, 2011; Morin and Liebhold, 2016; Liebhold et al., 2017).
Management-Forecasting and surveillance	Data from geographic information systems, forest inventory and analysis, and geospatial methods are used for forecasting defoliation by *L. d. dispar* (Liebhold et al., 1998; Liebhold and Tobin, 2008; Régnière et al., 2009).
Management-Treatments	Treatment efficacy is evaluated by using data from geographic information systems (Liebhold et al., 1996) or egg mass surveys (Liebhold et al., 1991). Populations are controlled through mating disruption with sex pheromone (Leonhardt et al., 1996; Onufrieva et al., 2019). Insecticides (Liebhold and McManus, 1999) and silvicultural treatments (Muzika and Liebhold, 2000; Muzika, 2017) have also been used in management.
Management-Execution and evaluation of the Slow-the-Spread program	An intensive Slow-the-Spread program has been implemented successfully in the United States for nearly 20 years (see text for details (Leonard and Sharov, 1995; Leuschner et al., 1996; Sharov et al., 1998, 2002a,b; Sharov and Liebhold, 1998; Leonard, 2007; Tobin and Blackburn, 2007)).

scale in 1992 (in four US states: Michigan, North Carolina, Virginia, and West Virginia), but was expanded and became operational in 2000 to include the entire expanding front (McManus, 2007). The theoretical underpinnings of the program include a reliance on historical data analysis of the invasive spread of European gypsy moth in North America (Liebhold et al., 2007) and the realization that spread has been facilitated by processes such as stratified diffusion or colony coalescence, whereby accidental movement of life stages by humans ahead of the invading population front initiate isolated population foci that coalesce and expand the front (Sharov and Liebhold, 1998; Liebhold et al., 2007). This process can be disrupted (slowed) by annual aggressive aerial

treatments at newly discovered foci, primarily with sex pheromone (mating disruption) targeting adult males, or to a lesser extent with *Btk* targeting larvae (Onufrieva et al., 2019). Detection trapping of male moths (Sharov et al., 1996a, 2002b) is critical for characterizing the new foci for treatment. The modern gypsy moth STS program is administered and executed through a foundation (Gypsy Moth Slow the Spread Foundation, Inc.; McManus, 2007) with technical leadership provided by the USDA Forest Service (http://www.gmsts.org/).

8 Conclusion and future trends

A large body of recent research has quantified the direct response of native and invasive forest insects to recent changing temperatures, in addition to indirect effects due to changes in temperature and precipitation patterns that stress host trees. In many cases, recent climatic changes have been positively correlated with range shifts northward and increased tree mortality within historic ranges. Predictions of future responses are mixed depending on the insect species and type of model used (i.e., correlative or process-based). Although warming temperatures drive model predictions for northward range expansion in most cases, range retractions of southern distributions are predicted for some species, a result of disruptions in cues for seasonality traits such as diapause and developmental rates and thresholds. Adequate predictions of future range expansions and insect-associated tree mortality events will benefit from research that quantifies (1) thermally dependent traits for use in process-based projection models, (2) climate effects on critical community associates and trophic interactions, and (3) adaptive potential of forest insects in a rapidly changing climate.

Describing and harnessing heritable genetic variation in tree resistance to native and invasive insects are becoming recognized as important aspects of future forest management. Recent advances in resistance screening techniques based on non-destructive spectrometric screening tools and modern –omics approaches provide avenues for phenotyping in the field. Research focused on intensive resistance screening can facilitate tree breeding programs to exploit naturally occurring variation in traits that confer resistance to specific native and invasive species.

Survey and detection are critical aspects of native and invasive forest insect management, including early detection of new outbreak foci so that tactics can be applied to maintain or reduce population levels below Allee thresholds for mating success. This is particularly important in slowing the spread of invaders (see below) and native defoliators. A variety of techniques have proven successful including the application of semiochemicals, used in conjunction with traps of varying colors and types, girdled trap trees, and genomic techniques for enhanced identification and monitoring of invasive

species. The use of drone aircraft equipped with high-definition sensors and photographic equipment offers a new platform for survey and detection of forest insect–caused tree mortality.

Following detection, integrated biocontrol strategies are currently being evaluated for their direct impact on forest insect populations. With invasive insects in particular, strategies are aimed at disrupting, or slowing, population expansion fronts. For example, a recent large pilot study to reduce spread of the invasive emerald ash borer, SLAM, employs a combination of tactics including girdled ash trees, regulatory control, public outreach, tree removal, and insecticide treatments. For defoliators, aerial spray treatments with multiple products, including sex pheromones for mating disruption and a bacterium *Bacillus thuringiensis* that causes larval mortality, have been shown to suppress specific populations in North America. Release of natural enemies has also proven successful for some native and invasive defoliator species in North America and Europe. Similar tactics are showing promise or are under evaluation for management of native and invasive bark beetle species, including release of predatory beetles (*Rhizophagus grandis*) in Europe and China, and use of the fungus *Beauveria bassiana* for controlling populations of *Dendroctonus* in North America and the European spruce beetle in Europe. Other direct control measures for bark beetles include new formulations and injection methods of insecticides, and development and commercialization of semiochemical formulations and delivery methods to disrupt adult aggregation.

Indirect control measures using silvicultural strategies have also proven efficacious for regulating multiple forest insect species, including non-native invaders. Recent research suggests that thinning stands is effective for increasing resistance to several bark beetle species in North America even during significant drought years. Maintaining high tree age and species diversity, including planting of tree species that are not hosts for particular insect species, has been associated with slower expansion rates of defoliators. Following successful tree breeding programs, planting and maintaining resistant genotypes on the landscape will be a long-term strategy for managing native and invasive forest insect species.

9 Where to look for further information

- A few general references describing climate effects on forest insects, including predictions and management options, are described in Bentz et al. (2010, 2019), Netherer and Schopf (2010), Règniére et al. (2012), Weed et al. (2013), Ayres and Lombardero (2018), and Pureswaran et al. (2018).
- The impact of drought on tree mortality and forest insects is reviewed by Jactel et al. (2012), Allen et al. (2015), and Kolb et al. (2016).

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- Garnas (2018) provides a review of insect plasticity and potential response to rapid climate change.
- The importance of understanding host tree resistance in invasive insect-plant interactions is summarized in Villari et al. (2016) and Schowalter et al. (2018), and Telford et al. (2015) and Sniezko and Koch (2017) provide reviews of harnessing natural genetic variation for breeding trees and managing forest insects.
- Aukema et al. (2010, 2011), Liebhold et al. (2017), and Poland et al. (2019) provide overviews of invasive forest insect biology, ecology, impact, and management.
- Fettig and Hilszczański (2015) provide an overview of management strategies for conifer bark beetles.
- Seybold et al. (2018) provide a synthesis of the concepts involved in semiochemical-based management of bark beetles with case studies of western North American species.

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