Jeremy D. Allison
Timothy D. Paine
Bernard Slippers
Michael J. Wingfield *Editors*

Forest Entomology and Pathology

Volume 1: Entomology

Springer

Jeremy D. Allison · Timothy D. Paine ·
Bernard Slippers · Michael J. Wingfield
Editors

Forest Entomology and Pathology

Volume 1: Entomology

Springer

Editors
Jeremy D. Allison
Natural Resources Canada
Sault Ste. Marie, ON, Canada

Bernard Slippers
Forestry and Agricultural Biotechnology
Institute
University of Pretoria
Hatfield, South Africa

Timothy D. Paine
Department of Entomology
University of California
Riverside, CA, USA

Michael J. Wingfield
Forestry and Agricultural Biotechnology
Institute
University of Pretoria
Hatfield, South Africa

Chapter 19
Monitoring and Surveillance of Forest Insects

Eckehard G. Brockerhoff, Juan C. Corley, Hervé Jactel, Daniel R. Miller, Robert J. Rabaglia, and Jon Sweeney

19.1 Introduction and Overview

Monitoring of insect populations is widely used in entomology in the context of biodiversity studies, as an aspect of pest management, and for the detection of non-native invasive species (e.g. Prasad and Prabhakar 2012; Rabaglia et al. 2019; Seibold et al. 2019). Here we focus on monitoring and surveillance of forest insect 'pests' as well as the detection of non-native invasive species. In general, monitoring is undertaken to (i) obtain information on the presence or abundance of particular species; (ii) study their phenology (e.g. oviposition or flight periods); (iii) predict pest population size, spread and damage; or (iv) to determine if pest management activities such as insecticide treatments or mating disruption are required. These activities are critical aspects of integrated pest management (IPM) programs (Ravlin 1991; Ehler 2006; Chapter 17, this volume).

E. G. Brockerhoff (✉)
Swiss Federal Research Institute WSL, Birmensdorf, Switzerland
e-mail: eckehard.brockerhoff@wsl.ch

J. C. Corley
IFAB (INTA EEA Bariloche-CONICET) and Departamento de Ecología, Universidad Nacional del Comahue, Bariloche, Argentina

H. Jactel
INRAE, University of Bordeaux, BIOGECO, Cestas, Bordeaux, France

D. R. Miller
USDA Forest Service, Southern Research Station, Athens, GA, USA

R. J. Rabaglia
USDA Forest Service, State and Private Forestry, Forest Health Protection, Washington, DC, USA

J. Sweeney
Natural Resources Canada-Canadian Forest Service, Atlantic Forestry Centre, Fredericton, NB, Canada
e-mail: jon.sweeney@nrcan-rncan.gc.ca

Insect monitoring and surveillance can be done with a variety of methods including physical surveys, the use of insect traps, molecular methods, as well as aerial surveys and remote sensing (Prasad and Prabhakar 2012; Poland and Rassati 2019). Physical field surveys (i.e. by direct observation) focus on insect life stages, characteristic damage symptoms on host plants (e.g. defoliation) or other noticeable signs. Such surveys usually involve a combination of observations in the field, collecting and counting specimens, and recording and analyzing these data. Tools that have long been used to facilitate and standardize insect 'sampling' include sweep-nets and tree-beating sheets (e.g. Morris 1960; Harris et al. 1972). However, these methods are labor-intensive, time-consuming, and can only sample species and life stages that are present at the time when the activity is undertaken by a person in the forest.

An alternative method that is widely used and often more efficient involves the use of insect traps that are based on a variety of mechanisms that draw insects to traps and/or intercept their flights. There is a wide range of trap types such as passive interception traps, light traps, colored sticky traps, and traps baited with certain chemical attractants (e.g. Muirhead-Thompson 1991). In recent years, molecular methods have become increasingly important not only for diagnostic purposes (i.e. species identification) but also for insect monitoring. For example, analyzing eDNA collected from plant surfaces can be a very effective method to detect the presence of target species in an area (Valentin et al. 2018). Remote sensing and aerial surveys are useful for monitoring insect damage across larger geographic areas and where forest access on the ground is limited (Hall et al. 2016; Stone and Mohammed 2017).

Monitoring insects is a very broad and complex subject. This chapter focusses on some of the more important methods to provide an overview of the objectives and applications of monitoring and surveillance of forest insects. These are illustrated with several case studies on monitoring and surveillance of prominent forest insects.

19.2   Monitoring Insect Populations and Damage

There is no single monitoring method that is suitable for all species and purposes. If and how monitoring is done ultimately depends on one's objectives and the availability and suitability of monitoring tools for the target species. Some species can be easily observed because their damage or other signs are highly visible by a trained observer and sufficiently specific. Other insects are rather cryptic and difficult to observe, for example because they are feeding under the bark or in the wood of trees. In such cases, alternative methods such as attractant-baited traps can be very helpful if effective attractants and traps for the target species are available. In this section we introduce the most common conventional monitoring methods.

19.2.1 Ground-Based Monitoring Methods for Insect Life Stages, Damage Symptoms and Other Signs

19.2.1.1 Visual Surveys for Insect Life Stages

Field surveys for eggs, larvae, pupae or adults of target species are a common practice for many species. For example, in the United States, egg masses of spongy moth (*Lymantria dispar*, Erebidae) are counted to determine whether infestation levels are so high that treatments may be necessary to prevent defoliation (Liebhold et al. 1994) (Fig. 19.1). Counting egg masses on tree trunks and branches can be done from the ground, ideally during winter when there is no foliage to obscure egg masses and to provide sufficient lead time for planning management actions. Several procedures have been developed to obtain reliable estimates of spongy moth population density, such as the "fixed-radius" plot method where all trees within several 100 m^2 plots are counted and the average density of egg masses is calculated (Liebhold et al. 1994). Leaf miners and gall makers are also easily identified based on their characteristic symptoms and surveys looking for these symptoms are feasible. Other insects and life stages are commonly sampled with specific tools developed for this purpose.

Fig. 19.1 Egg masses of spongy moth on an oak tree trunk. Credit: Milan Zubrik, Forest Research Institute—Slovakia, Bugwood.org

19.2.1.2 Tools for Sampling Insects

Surveys for foliage-feeding insects are often done using 'beat sheets' in which a pole is used to beat branches and dislodge specimens onto a drop sheet where they can be collected and counted. The number of replicates depends on the size of the area of interest and the sampling accuracy required, but at least three trees should be sampled (Harris et al. 1972). This method has been used, for example, to sample and study the host range of conifer aphids in New Zealand (Redlich et al. 2019) and to sample predators of hemlock woolly adelgid (*Adelges tsugae*, Adelgidae), a severe pest of Eastern hemlock (*Tsuga canadensis*) in eastern North America (Mayfield et al. 2020) (Fig. 19.2). Suction traps using air suction are often used for sampling insects dispersing in large numbers such as aphids and thrips (e.g. Allison and Pike 1988) but they are used less with forest insects. Insects that are concealed inside wood or other plant tissues (e.g. bark beetles, wood borers) may be sampled by enclosing sections of tree stems, branches and twigs in emergence cages or by collecting tree parts and incubating them in chambers to collect the emerging adults (Ferro and Carlton 2011; Chapter 3, this volume).

Fig. 19.2 Using a beat sheet to sample *Laricobius* beetles, predators of the hemlock woolly adelgid. Credit: A. Mayfield, USDA Forest Service

19.2.1.3   Surveys for Symptoms and Signs

The extensive mortality of pines caused by the southern pine beetle (*Dendroctonus frontalis*, Scolytinae) in the southern United States is highly visible. To monitor earlier signs of attack, before trees have succumbed to the beetles and when management interventions are still feasible to avert damage, surveys of boring dust and 'pitch tubes' created by the resin response of attacked trees are an effective method (Billings 2011) (Fig. 19.3).

Monitoring for the presence and relative abundance of the pine processionary moth (*Thaumetopoea pityocampa*, Thaumetopoeidae), a serious defoliator of pines and a public health risk in southern Europe, is done by counting the easily visible silken winter nests made by larvae in the crowns of pine trees (Gery and Miller 1985) (Fig. 19.4) (see also the case study on the pine processionary moth below).

19.2.2   Insect Monitoring Using Traps

Ground-based visual surveys for insect life stages or symptoms of attack may be labour-intensive and time-consuming. Trapping can be more effective, especially if an effective attractant is available that increases the catch rate and specificity of traps. Trapping is widely used for insect monitoring and there is a variety of trap types and mechanisms that may be generic or optimised for particular target species (e.g. Muirhead-Thompson 1991; Häuser and Riede 2015).

Fig. 19.3 'Pitch tubes' on a loblolly pine trunk caused by southern pine beetle attack. Credit: James R. Meeker, USDA Forest Service, Bugwood.org

Fig. 19.4 Nests of the pine processionary moth on Scots pine in Switzerland. Credit: Beat Forster, Swiss Federal Institute for Forest, Snow and Landscape Research, Bugwood.org

19.2.2.1 Passive Traps

Passive traps do not use any particular mode of attraction but simply intercept and trap insects as they are moving about. Examples include pitfall traps (cups buried at ground level that are filled with a liquid preservative that trap walking insects), Malaise traps (tent-like structures that intercept flying insects and trap them in a jar filled with a liquid preservative), window traps and other types of flight intercept traps (see Häuser and Riede (2015) and Knuff et al. (2019) for further references and Fig. 19.5). These trap types are commonly used for biodiversity studies but less so to sample forest pests, partly because they are non-specific and collect large numbers of insects from many species, which results in considerable sorting effort. Such passive traps are typically less sensitive than traps that involve some means of attraction.

19.2.2.2 Traps Involving Attraction of Insects by Light or Color

There are many trap types that attract insects with light, specific colors or silhouettes, chemical attractants (odorants such as insect pheromones and host plant volatiles), or a combination of two or more of these (Muirhead-Thompson 1991). Historically, light trapping was used for monitoring populations of insect pests that fly at night (such as moths and certain beetles). An advantage of light traps is that they capture both males and females (whereas traps baited with sex pheromones typically capture only males). Light traps used to require access to the electricity grid (i.e. mains power) which prohibited their use at most field sites but this is less of a problem now

Fig. 19.5 A malaise trap for capturing flying insects. Credit: D. Miller, USDA Forest Service

with the wide availability of portable power sources. Still, today light trapping is used mainly in biodiversity studies because other methods are more species-specific and more effective.

Trap color on its own is exploited, for example, in yellow traps which are used mainly for monitoring agricultural and greenhouse pests. However, trap color can also affect captures of certain forest insects by synergizing attraction of bark beetles to chemical attractants (e.g. Kerr et al. 2017). Several species of longhorned wood boring beetles (Cerambycidae) respond more to black traps than clear or white traps (Campbell and Borden 2009; Allison and Redak 2017) while other cerambycids and jewel beetles (Buprestidae) are attracted to bright green traps or purple traps (Rassati et al. 2019). Bright green or yellow sticky traps mimic the color of foliage and can be used to monitor defoliators such as the beech leaf-mining weevil (Goodwin et al. 2020). Certain trap colors may also reduce catches of non-target species (e.g. Sukovata et al. 2020).

19.2.2.3 Traps Baited with Pheromones and Host Plant Volatiles

The most widely used traps for forest insects are those baited with odorant lures such as pheromones and host plant volatiles. Pheromones are chemicals that insects release for communication with conspecifics (Howse et al. 1998). The best-known pheromones are moth 'sex pheromones' that are released by females to attract males. Many bark beetles (Scolytinae) release 'aggregation pheromones' that facilitate aggregation on host trees (Byers 1989), and many wood boring longhorned beetles (Cerambycidae) emit 'sex-aggregation pheromones' that attract both sexes, primarily for mating (Hanks and Millar 2016). There are several other types of pheromones (Howse et al. 1998) but they are less important in the context of monitoring.

The chemical structures of pheromones have been identified for many forest insects, especially those of economic importance, and synthetic lures may be commercially available (El-Sayed 2020). Pheromones are often composed of several components and are more or less specific to their species or genus, especially in moths (Lepidoptera) (Löfstedt et al. 2016). For example, traps baited with the main pheromone component of spongy moth (7,8-epoxy-2-methyloctadecane, a 19-carbon epoxide), also known as 'disparlure', catch mainly spongy moth and several congenerics and are widely used for monitoring and detection purposes. The complete blend of the pheromone of spongy moth contains minor components which increase its species specificity (Gries et al. 1996). On the other hand, longhorned wood boring beetles share many of the same sex-aggregation pheromone components. For example, traps baited with racemic 3-hydroxy-2-hexanone can attract several species of Cerambycidae (Millar and Hanks 2017).

Not all insect species use pheromones, and those of many other species remain to be identified. However, host plant volatiles may be used as an alternative attractant for plant-feeding insects because many species use these cues when searching for their hosts. For example, many conifer-feeding bark beetles and woodborers are attracted to alpha-pinene and ethanol, two components that are commonly associated with conifers. Hence, alpha-pinene and ethanol are used to monitor beetles associated with conifers including species of *Arhopalus* (Cerambycidae), *Hylastes* and *Ips* (Scolytinae) (Brockerhoff et al. 2006; Miller and Rabaglia 2009). Likewise, many ambrosia beetles are attracted to ethanol which is an effective lure for species such as *Xyleborus* spp. and *Xylosandrus crassiusculus* (Scolytinae) (Miller and Rabaglia 2009; Reding et al. 2011). Plant volatiles that assist insects with finding their host plants are often referred to as 'kairomones'. While pheromones are 'information chemicals' that are involved in intraspecific communication, kairomones are used as cues for interspecific interactions.

Traps used with pheromones and host plant attractants come in a variety of shapes, sizes, and colours. They use different mechanisms for trapping insects either on a sticky surface or in a collection jar that is easy to enter for an insect but very difficult to exit (effectively a one-way entry). Multiple-funnel traps (also called Lindgren funnel traps after their inventor) are used mainly for bark beetles (Lindgren 1983). They consist of a stack of several funnels and a collection cup at the base (Fig. 19.6a). Panel traps are an alternative design that involves intersecting panels with a single funnel

and a collection jar at the base (Fig. 19.6b). These panel traps are typically used for longhorned beetles, weevils and bark beetles. A fluoropolymer may be applied to traps to make them more 'slippery' so that beetles can't hold on to the panel surface (Graham et al. 2010). Funnel and panel traps are mainly colored black so that they resemble the silhouette of a tree trunk, but they are available in other colors. For example, for monitoring emerald ash borer (*Agrilus planipennis*, Buprestidae), green funnel traps (with an attractant) are preferable (Poland et al. 2019). The most common trap design used for bark beetle monitoring in Europe is the so-called Theysohn slot-trap which is based on an alternative flight interception design (Fig. 19.6c).

Neither of these traps work well for Lepidoptera, Hymenoptera and other less 'robust' taxa with a comparatively soft cuticle. For these species, trap types with sticky surfaces are commonly chosen. Perhaps the most widely used of these is the Delta trap which has a roof-shaped design with a sticky substance either on the entire internal surface or on a removable sheet in the trap. A lure is placed inside the trap and insects attracted by this lure are trapped when they land on the sticky internal surface (Fig. 19.6d). An advantage of this design is that the captured insects are spread out on the sticky area which makes examining the catches easy, unless they need to be removed for closer inspection, which may be difficult. A potential disadvantage of delta traps is their propensity to become saturated with the target species. When that is a problem, bucket traps with a larger holding capacity can be used. Unwanted by-catch can be reduced by choosing traps colored green which attract fewer flower-visiting insects than yellow or white traps, for example (Sukovata et al. 2020).

19.2.3 Important Considerations for Trap-Based Monitoring Programs Targeting Bark and Wood Boring Beetles

There are many successful monitoring programs for bark and woodboring beetles in Europe, North America and elsewhere. For example, in Europe, trapping is widely used to monitor populations of the European spruce bark beetle (*Ips typographus*, Scolytinae), the most serious insect pest of spruce forests in Europe. The main purpose is to follow population trends, as described, for example, by Faccoli and Stergulc (2005). Typically, Theysohn slot-traps baited with pheromone (ipsdienol and methyl-butenol) dispensers are used to attract *I. typographus*, and the ratio of trap captures of the summer generation and the spring generation can be calculated to determine whether populations are growing or declining. However, there is some controversy about the extent to which trap captures reflect *I. typographus* population sizes and trends (see Sect. 19.4).

In the southern USA, forest managers use a trap-based monitoring system as part of an IPM program to manage the southern pine beetle (SPB), a major pest of southern pines (Clarke 2012). In the spring of every year, funnel traps baited with pheromone (frontalin) and kairomones (alpha-pinene and beta-pinene) are deployed

Fig. 19.6 Various traps used for insect monitoring and surveillance: **a** Lindgren-funnel trap. Credit: D. Miller, USDA Forest Service; **b** Panel trap with alpha-pinene and ethanol lures attached. Credit: J. Kerr, Scion, New Zealand; **c** Theysohn bark beetle trap. Credit: Gernot Hoch, BFW Institut für Waldschutz, Vienna, Austria; **d** Delta trap. Credit: Karla Salp, Washington State Department of Agriculture, Bugwood.org; **e** Sticky plate trap with pheromone lures in the center and a trapped pine processionary moth. Credit: Hervé Jactel, INRAe, France

at key locations in and around pine stands. Managers consider the number of SPB captured as well as the ratio of predators (the checkered beetle *Thanasimus dubius*, Cleridae) to SPB to determine if local epidemics are increasing, stable or collapsing. This information is used to determine the need for management efforts against SPB.

Operationally, the choice of trap type, lure type and trap position is a major concern for managers planning a trapping program, and these parameters depend on the target species. The efficacy of a trapping program for a single species or broad diversity can be affected by numerous factors such as trap location (canopy vs ground, forest

edge vs forest interior), trap type and color, and trapping period and duration (e.g. Brockerhoff et al. 2012; Dodds 2014; Flaherty et al. 2019; Sweeney et al. 2020). Managers need to be clear about their objectives for a trapping program as there is no single scheme that can target all species equally.

Relative species-specificity of lures can be achieved for some species such as the engraver bark beetle *Ips paraconfusus* (Scolytinae) that uses a combination of (−)-ipsenol, (+)-ipsdienol and *cis*-verbenol as its pheromone blend, while frontalin is a common pheromone for various species of *Dendroctonus* (Scolytinae) (Byers 1989). Traps baited with genus-specific monochamol lures are attractive specifically to sawyer beetles (*Monochamus* spp., Cerambycidae) in North America, Europe and Asia, although traps baited with the bark beetle pheromone ipsenol may be equally attractive for *Monochamus* species (Ryall et al. 2015; Miller et al. 2016).

To capture multiple species, blends of multiple attractants can be used. For example, blends of certain hexanediols and hydroxyketones are broadly attractive to numerous woodborers in the longhorn beetle subfamily Cerambycinae (Hanks and Millar 2016). Traps baited with the host plant volatiles alpha-pinene and ethanol are broadly attractive to many bark and ambrosia beetles (Miller and Rabaglia 2009). A combination of alpha-pinene and ethanol and bark beetle pheromones attracts numerous species of woodborers including *Monochamus* species as well as numerous species of bark and ambrosia beetles, and associated predators (e.g. Miller et al. 2013, 2015; Alvarez et al. 2016; Chase et al. 2018).

19.2.4 *Monitoring the Population Dynamics of Pine Processionary Moth with Pheromone Trapping*

The pine processionary moth (PPM) is the main insect defoliator of pine forests in southern Europe and North Africa (Roques 2015). Severe defoliations by PPM caterpillars feeding on needles result in reduced tree growth (Jacquet et al. 2012) and increase the risk of mortality (Jacquet et al. 2014). The larvae have urticating hairs which can cause serious health problems in people and domestic animals (Vega et al. 2011). PPM populations exhibit cyclic outbreaks (Li et al. 2015) and even though the year of the next peak infestation can be forecasted, the amplitude of defoliation remains unpredictable (Toïgo et al. 2017). It was therefore important to develop a reliable method for monitoring and predicting PPM infestation levels in order to warn forest users and implement necessary control measures such as applications of the toxin of *Bacillus thuringiensis* (*Bt)* when populations get too large.

The conventional population monitoring of PPM is based on counts of winter nests made by larvae in the tree crown (Gery and Miller 1985), but this is tedious and inaccurate in mature or dense pine stands. Pheromone trapping has been considered an alternative method and has proven highly effective in the field (Einhorn et al. 1983). To develop pheromone trapping as a reliable sampling technique, a suitable trap design and trap position had to be identified and it needed to be shown that

trap captures were indicative of actual population levels. Sticky plate traps hung at user-friendly heights of about 1.5 m above ground (Fig. 19.6e) appeared to be the most efficient (Jactel et al. 2006). It was also necessary to optimise the pheromone dose and the density of traps to improve the statistical correlations between mean trap capture and other measures of population density. Four sticky plate traps baited with 0.2 mg of the commercial pheromone ("pityolure") provide an accurate and cost-effective estimate of the total number of PPM per hectare (Jactel et al. 2006). This method was tested and further refined in a large operational trial in France (see Sect. 19.4).

19.2.5 Monitoring Populations of the Invasive Woodwasp Sirex Noctilio

Among the non-native invasive forest insects observed in commercial plantation forests in many southern hemisphere countries, the woodwasp *Sirex noctilio* F. (Siricidae) is probably the best known. The species is capable of widespread damage on cultivated pines within the invaded range, especially during population outbreaks (Lantschner and Corley 2015). *Sirex noctilio* is a woodboring species with a solitary lifestyle that infests pine trees. Following mating, females lay eggs by drilling holes in pine stems which they locate by following volatile cues associated with tree stress. During oviposition, the female introduces a symbiotic fungus (*Amylostereum areolatum)* and a phytotoxic venom which together can kill attacked trees (Slippers et al. 2015).

Population monitoring is an important aspect of *S. noctilio* pest management and is often carried out within the invaded range by looking for trees with signs of attack, rather than the insect itself. Attacked pines typically show crown chlorosis, and resin droplets on their stems resulting from oviposition by *S. noctilio.* Sequential sampling protocols and/or aerial surveys support estimations of tree damage and the application of control measures. However, sequential sampling is somewhat flawed as attacks are typically highly aggregated. This approach may underestimate attack levels, especially when populations are low such as in recently invaded sites (Carnegie et al. 2005; Lantschner and Corley 2015).

Alternatively, the trap-tree technique is used to detect early-stage populations. This consists of treating 4–10 trees with low doses of herbicide or careful girdling prior to the wasp flight season (Fig. 19.7). Foraging females are attracted to these artificially stressed trees which can then reveal the presence of *S. noctilio.* Felling of any attacked trees after the flight season may be necessary to avoid the build-up of local populations (Lantschner and Corley 2015). When billets (stem sections) from these trees are caged, the presence and abundance of natural enemies (especially parasitoids attacking the wood wasps) and their potential impact on the *S. noctilio* population can be estimated.

Fig. 19.7 Trap trees to attract Sirex wood wasps in a Pinus contorta plantation in Patagonia, Argentina. Credit: Juan Corley

Flight intercept traps (panel traps or funnel traps) baited with combinations of alpha-pinene and beta-pinene, which are also emitted by stressed trees, can be used to sample *S. noctilio* populations. However, trapping with these lures is usually not as effective as it is for many other insects (Batista et al. 2018). The development of new pheromone and kairomone lures which are based on attractive volatiles from conspecifics or from the wasp's fungal symbiont, may prove important as this type of lure can be highly specific and works well also at low population densities (Fernández Ajó et al. 2015).

The development of effective sampling methods to monitor *S. noctilio* populations within the invaded range is especially important since detecting small populations as early as possible during the invasion phase and understanding when and why *S. noctilio* populations increase is key to preventing regional spread and major economic impact in invaded areas. These should not only include effective trap and lure designs but also statistically valid sampling efforts, to provide quantitative data in diverse environmental conditions. This information is also needed to interpret the success of the control practices deployed.

19.3 Surveillance to Detect Invaders

Preventing the introduction of non-native species is the most effective and first line of defense, although some species may inevitably escape detection and become established. The greatest opportunity for eradication and cost-effective management is immediately after their introduction when their populations are still small and limited to a small area. Early detection followed by rapid assessment and response increases the likelihood of successful eradication or containment (Brockerhoff et al. 2010; Liebhold et al. 2016). There are a number of other purposes of surveillance including to demonstrate freedom from certain pests within an area (a potential requirement for international trade) and to verify the effectiveness of biosecurity measures (Kalaris et al. 2014).

Numerous methods and tools can be applied for surveillance and detection of non-native insects (e.g. Augustin et al. 2012; Kalaris et al. 2014; Poland and Rassati 2019). Many are similar to those used for monitoring native insects (see Sect. 19.2). But there are several key differences: (i) the main initial goal is to detect the *presence* of a non-native species, whereas determining its population size and spatial extent (i.e. delimitation) is a subsequent step; (ii) there is a rather large number of potential invaders, and surveillance often aims at detecting any of multiple species, although some programs are aimed at just one specific unwanted species; and (iii) one is virtually looking for a needle in a hay stack as the aim is to find a small population that could be anywhere. Consequently, methods that are highly sensitive and can cover large areas are preferable. However, if the identity of the target is unknown, methods suitable for a wide range of species are needed. For both cases, trapping with suitable trap type and lure combinations is a preferred option (e.g. Quilici et al. 2012). Below we describe two trapping programs to detect invaders (for spongy moth and non-native bark- and woodboring beetles). But as trapping can only target a limited number of species, more generic surveillance methods that can detect a wider range of species are also needed. Physical searching by trained biosecurity specialists to detect new non-native species is being carried out in several countries, often with a focus on high-risk sites. Engagement of the wider public in surveillance activities can also be highly effective. Examples of these approaches are given below.

19.3.1 High-Risk Site Surveillance

Early detection of non-native species is very important for successful responses to detections. Because the resources for surveillance are limited, efforts need to be focused on locations where non-native species are most likely to arrive and become established. By definition, such locations can be characterized by the likelihood of arrival of non-native pests and by the likelihood of establishment at those sites.

Insights about the likelihood of arrival can be gained from information about trade patterns, particularly regarding the volume and destinations of those types of imports

that are known to be associated with species of concern (Colunga-Garcia et al. 2013; Kalaris et al. 2014). These sites tend to be concentrated around commercial and industrial areas, rather than in the forests that are at risk. The surroundings of air and sea ports are also considered high-risk sites although with today's fast and often containerized trade, there is more opportunity for organisms to escape at the eventual destinations of shipments, rather than at ports where shipments pass through. Larger metropolitan areas that are the destination of a large proportion of imported goods and insects transported with these (Branco et al. 2019) are focus areas for surveillance. Therefore, human population size and density can be used as simple proxies if more detailed information about trade flows is not available.

Sites that warrant particular attention are those where imported high-risk commodities arrive such as live plants (e.g. nurseries and garden centers) and wood packaging materials (e.g. recipients of large volumes of paving stones and tiles that are typically packed with pallets and case wood) (Liebhold et al. 2012; Haack 2006). Such information has been used to identify potential hotspots for invasion pressure in the United States where surveillance efforts should be particularly intensive (Colunga-Garcia et al. 2013). Similar concepts have been developed and implemented in other countries. For example, the New Zealand government operates a high-risk site surveillance system in the main urban areas with thousands of transect inspections every year, focusing on urban trees and parks near commercial and industrial areas as well as campsites in natural areas where overseas tourists may introduce pests inadvertently (Bulman 2008; Stevens 2008).

19.3.2 *Engaging the Public in Surveillance Activities*

Although most members of the public are not experienced in insect identification and detection of non-native species, they are far more numerous than trained professional surveillance staff. It is not uncommon for citizens to notice unusual tree damage and unusual insects in their neighborhood. Consequently, the public should be considered in a surveillance framework as contributing to 'passive surveillance' (e.g. Froud et al. 2008; Hester and Cacho 2017). In New Zealand, there is an established system by which the general public can contribute and report suspicious finds of insects and other species via a toll-free phone number, with about 4,000 notifications per year (Froud et al. 2008). Approximately 8% of all detections of new incursions were reported by the general public, slightly more than those reported by industry. The public is especially encouraged to assist with reporting particular high-risk species and New Zealand's biosecurity authority runs campaigns with newspaper advertisements, tv commercials and social media posts such as the "Catch it - call us" campaign (Fig. 19.8).

The development of a biosecurity board game targeted at both children and adults has proven useful as another way to increase the awareness of the public about biosecurity issues, including the purpose of surveillance. To enhance the ability of the public to identify and report potential biosecurity threats, mobile phone-based
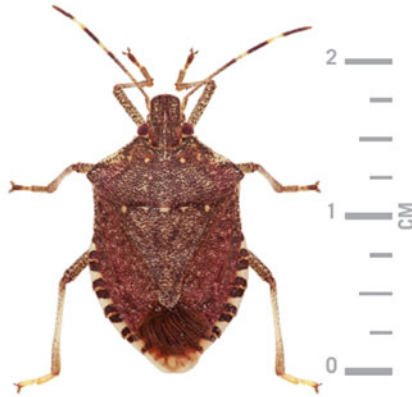
Fig. 19.8 Advertising used for the "Catch it - call us" campaign by New Zealand's national biosecurity agency MPI to encourage reporting finds of an invasive insect. *Source* https://twitter.com/MPI_NZ/status/662489108065812480

apps have been developed including 'Wild Spotter' in the United States (www.wil
dspotter.org, Wild Spotter 2020), 'Observatree' in the UK (https://www.observatree.
org.uk) and 'Find-a-Pest' in New Zealand (www.findapest.nz, Pawson et al. 2020).
The Find-a-Pest app is effective in reducing the number of false positives (i.e. reports
that were of no concern). False positives can be a problem because they occupy the
attention and time of biosecurity officials.

19.3.3 Spongy Moth Detection Trapping

The program to detect new infestations of spongy moth along its invasion front and in
uninfested regions of the United States is perhaps the largest trap-based pest detection
and surveillance program in the world. Approximately 250,000 pheromone-baited
spongy moth traps are placed annually by the Animal and Plant Health Inspection
Service of the United States Department of Agriculture (USDA APHIS) to detect new
populations (USDA 2019). In addition, the USDA Forest Service deploys more than
100,000 traps as part of the spongy moth 'slow the spread' program (Sharov et al.
2002; Bloem et al. 2014). The goal of this program is to minimize the rate of spongy
moth spread into uninfested areas in central and southern US forests. Traps along the
expanding population front are used to identify newly established populations. Any
such populations are then treated to prevent them from growing and coalescing into
larger infestations. This approach has successfully reduced the spread rate of spongy
moth by > 70% from the historical spread rate of approximately 21 km per year to an
average of approximately 6 km per year between 1990 and 2005 (Fig. 5.11a in Tobin
and Blackburn 2007), and has a projected benefit-to-cost ratio of approximately
3:1 by delaying the onset of impacts and management expenditures that occur as
spongy moth invades new areas (Tobin and Blackburn 2007). This intensive targeted
surveillance has enabled the very high success rate of eradications of spongy moth
populations, close to 100%, that were detected (Kean et al. 2020).

A similar but smaller detection program is carried out in New Zealand and in
Australia. But intensive surveillance is costly and it would be difficult to fund similar
programs multiple times for a large number of potential pests. However, it is possible
to add lures for other species to spongy moth traps, and this was examined for pairs
of spongy moth and 18 other well-known pest moths (Brockerhoff et al. 2013). Lures
for more than half of the species could be combined without a substantial reduction
in trap sensitivity for either species, and most of the other pairs still caught moths
in numbers sufficient for detection purposes. Therefore, combining compatible lures
for multiple target species could increase the number of targeted species without
greatly increasing the cost of such surveillance programs.

19.3.4   Trapping Programs to Detect Non-Native Bark Beetles and Wood Borers

Bark beetles (Scolytinae) have long been a focus of surveillance programs for non-native forest insects. For example, following the detection of the European pine shoot beetle (*Tomicus piniperda*, Scolytinae) in 1992 in Ohio, a surveillance trapping program was initiated in 1993 in the northeastern United States to enable early detection of other non-native bark beetles (Bridges 1995). Trapping with attractant-baited traps focused on high risk sites including areas near ports, importer warehouses and lumberyards. In 1996, when the first established population of the Asian longhorned beetle (*Anoplophora glabripennis*, Cerambycidae) outside its native range was discovered in New York City (Haack et al. 2010), the threat posed by longhorned beetles became more obvious. There was a growing realization that the large-scale use of solid wood packaging material (WPM) in international trade was a dangerous pathway that made invasions of both wood borers and bark beetles more likely. Between 1985 and 2005, established populations of 25 exotic species of bark beetles and wood borers (Scolytinae, Cerambycidae, Buprestidae) were detected in the United States (Haack 2006) and most of these probably arrived with WPM. Subsequently, a nationwide surveillance trapping program for bark beetles and ambrosia beetles was initiated in the United States (see Sect. 19.3.5).

Several other countries have developed surveillance programs for bark and wood-boring insects, albeit on a smaller scale. For example, such a program was trialed in New Zealand from 2002–2005 using funnel traps baited with host plant attractants and/or bark beetle pheromones, targeting a range of conifer-infesting wood borers and bark beetles (Brockerhoff et al. 2006). Although that particular surveillance program did not lead to the detection of any species not already known to be present, it did confirm the suitability of the approach as numerous non-native Scolytinae and Cerambycidae were trapped near seaports, airports, cargo unloading sites, and in forests near such locations. The surveillance trapping program for bark beetles and wood borers in New Zealand was discontinued mainly because there was uncertainty whether expenditures for the program were justified. However, a benefit–cost analysis carried out later indicated that such a surveillance program is expected to provide economic net benefits even at a high trap density because the economic benefits of early detection, a greater likelihood of successful eradication and less pest damage, likely exceeded the costs of the surveillance program (Epanchin-Niell et al. 2014).

Intercept panel traps or multiple-funnel traps (described above) are used in most detection programs. However, Malaise traps may be more effective in the detection of numerous species of bark and wood boring beetles (Dodds et al. 2015) but there is a trade-off because Malaise-type traps are about five times more expensive than intercept or funnel traps. In addition, Malaise traps tend to capture many more non-target species and consequently require more labor for sorting samples. Given the apparent variability in trapping efficiency even at short distances, detection programs might be more cost effective by using a larger number of panel or funnel traps than Malaise-type traps. Another method that may be suitable for increasing the efficiency

of detection trapping is to use a combination of lure blends so that each trap targets multiple species (rather than using separate traps each baited only for a particular species) (Chase et al. 2018; Fan et al. 2019; Rassati et al. 2019). This would either reduce the number of traps needed, or it would lead to an increased number of traps available for detecting particular species. There is a potential disadvantage of using lure blends in that it may reduce the number of insects caught of some species (Miller et al. 2017). However, for the purpose of detection, it is only necessary to trap at least one individual of a target species, so this disadvantage may be tolerable.

19.3.5   *Early Detection of Bark and Ambrosia Beetles in the US*

Bark and ambrosia beetles (Scolytinae) are some of the most important insects affecting forests in North America, and are the most commonly intercepted group of beetles at US ports of entry (Haack 2006). From 1984–2008, more than 8,000 interceptions of bark and ambrosia beetles, from 85 different countries, were reported at US ports (Haack and Rabaglia 2013). To increase the likelihood of early detection of such beetles, the USDA Forest Service began a pilot project in 2001 (Rabaglia et al. 2008) and then implemented in 2007 a national project for the early detection and rapid response (EDRR) of non-native bark and ambrosia beetles across the US (Rabaglia et al. 2019). The target species were selected based on their frequency of interception, the potential damage a species may cause in the US, and the availability of effective traps and lures for the species. The Scolytinae species selected were *Hylurgops palliatus*, *Hylurgus ligniperda*, *Ips sexdentatus*, *Ips typographus*, *Orthotomicus erosus*, *Pityogenes chalcographus*, *Tomicus minor*, *Tomicus piniperda*, *Trypodendron domesticum*, and *Xyleborus* species.

Three Lindgren funnel traps were used at each survey location, and each trap was baited with one of the following three lures or lure combinations: (i) ultra-high release (UHR) ethanol lure only, a general attractant for woodboring insects in hardwood and some coniferous hosts, (ii) UHR alpha-pinene and UHR ethanol lures together, which are general attractants for woodboring insects in coniferous hosts (Miller and Rabaglia 2009), and (iii) a three-component exotic *Ips* lure of ipsdienol, cis-verbenol and methyl-butenol, a specific combination for *I. typographus* and several other conifer-feeding exotic bark beetles (Bakke et al. 1977). Trapping began based on local phenology of bud break and knowledge of early emergence of bark and ambrosia beetles, from late February to early May, depending on the State, and lasted typically for 12 weeks.

Since 2010, the project focused on five high-risk states (California, Florida, Georgia, New York, and Texas), based on interceptions at ports-of-entry, the number of established non-native species, the amount of forest land, and transportation corridors. Other states were surveyed only every 3–7 years, depending on their risk and available funding. Within each state, trapping was carried out in wooded areas or

parks near high-risk sites where potentially infested solid wood packing material (e.g. wooden crates and pallets) were imported, stored, or recycled. Taxonomists identified all of the bark and ambrosia beetles and the data were shared at www.bar kbeetles.info.

More than 840,000 specimens of bark and ambrosia beetles had been collected and identified in forty-eight states (including Alaska and Hawaii), Puerto Rico, and Guam from 2007–2016 (Rabaglia et al. 2019). Within the continental U.S., the survey captured specimens of approximately 300 species out of the approximately 550 that occur in the U.S. Forty-three of the species collected were non-native species established in the U.S. The three most common species in traps were *Xyleborinus saxesenii*, *Xylosandrus crassiusculus*, and *Xylosandrus germanus*, three well-established non-native species with strong responses to ethanol-baited traps.

The primary goal of EDRR is the early detection of species new to North America. In the first few years of the pilot phase of EDRR, five species of scolytines new to North America were found in traps, and since 2007, three additional species new to North America were found: *Xyleborinus octiesdentatus*, *Xylosandrus amputatus*, and *Xyleborinus artestriatus* (Rabaglia et al. 2019). Assessments and follow up surveys to delimit the distribution of the new species were conducted soon after but these beetles were established over large areas and eradication was not feasible. Eradication of xyleborine ambrosia beetles, such as these three species, can be particularly challenging. Their cryptic nature, wide host range (these species breed in most hardwood trees), and their inbred, polygynous biology, allows them to go undetected and to quickly spread from just a few individuals.

It is likely that some, if not most, of the species newly detected during the beginning years of EDRR were present in the U.S. for decades. These legacy species were soon detected with the start of surveys such as EDRR. Since 2010, there have been no detections of species new to North America in EDRR traps. It is possible that all non-native species established in the states surveyed before 2010 have been detected and any new detections will be of recent introductions allowing for a more effective rapid response. It is also possible that the implementation of international protocols, such as ISPM 15, and awareness of the risk of moving wood products has reduced the number of wood boring insects introduced into the U.S.

19.3.6 Development of Survey Tools for an Invasive Longhorn Beetle in Canada

The brown spruce longhorn beetle (BSLB), *Tetropium fuscum* (Cerambycidae)*, native to Europe, was discovered in Halifax, Nova Scotia, Canada in 1999, infesting mature red spruce (Smith and Hurley 2000). About one third of trees displaying signs of resin flow on the trunk and spheroidal exit holes were dead but most were alive and appeared healthy, suggesting BSLB was successfully colonizing and killing trees (O'Leary et al. 2003). The Canadian Food Inspection Agency (CFIA) declared

BSLB a regulated quarantine pest in spring of 2000 and led a multiagency "BSLB task Force" in a survey and eradication program. The regulated area was delimited using intensive ground surveys and the visual signs of infestation, examining > 52,000 conifers on > 47,000 residential properties in greater Halifax in 2000.

Lindgren funnel traps (Lindgren 1983) baited with the same three lure combinations used by the EDRR program in the US (i.e. ethanol and alpha-pinene, ethanol alone, or a three-component exotic *Ips* lure) had been deployed in Halifax by CFIA since 1995 for exotic woodborer surveillance, but had failed to detect BSLB. Thus, members of the Task Force collaborated to develop survey tools to detect spread of BSLB and monitor the progress of the eradication program. Decks of freshly cut spruce logs (Post and Werner 1988) were deployed along major highways from Halifax in 2000–2002. Log decks detected BSLB in two new locations outside of the regulated area but were labor-intensive and slow. In 2003, log decks were replaced by intercept panel traps (Czokajlo et al. 2001; de Groot and Nott 2001) baited with a synthetic "spruce blend" lure, consisting of five major monoterpenes emitted from infested spruce (Sweeney et al. 2004). Adding an ethanol lure increased detection rates (Sweeney et al. 2004, 2006) and from 2004–2006, these baited traps detected BSLB in 25 sites outside of the regulated area, prompting CFIA to expand the regulated area in spring of 2007.

In 2006, Silk et al. (2007) identified a male-produced sex-aggregation pheromone, (*E*)-6,10-dimethyl-5,9,-undecadien-2-ol ("fuscumol"), that synergized attraction of both sexes of BSLB when combined with spruce blend and ethanol. In 2007, operational surveys with the more sensitive pheromone-baited traps detected BSLB in 16 sites outside of the newly expanded regulated area, and CFIA switched the goal from eradication to slowing the spread (CFIA 2017). By spring of 2015, BSLB had been detected in more than 100 sites outside of the 2007 regulated area and CFIA declared the entire province of Nova Scotia infested (CFIA 2017).

This case study highlights the importance of inter-agency collaboration and rapid technology transfer in the development of operational survey tools. It also highlights the critical need for effective survey tools for early detection when containment or eradication of an invasive species is still feasible (Brockerhoff et al. 2010; Tobin et al. 2014; Liebhold and Keen 2018).

19.4 Making Sense of Trap Catch Data, and Statistical Considerations

19.4.1 Relationships Between Trap Catch and Local Population Size

The relationship between trap catch and local population density of forest insects, tree damage or tree mortality is not always strong. For example, while pheromone-baited traps can be useful for determining whether *I. typographus* populations are growing

or declining (Faccoli and Stergulc 2006), and low catches were indicative of low levels of damage occurring, high catches were not well correlated with infestation levels near traps (Lindelöw and Schroeder 2001). In another study, no relationship at all was found between trap catch of *I. typographus* and attacks of trees nearby (Wichmann and Ravn 2001). Likewise, in North America, a study of western pine beetle (*Dendroctonus brevicomis*) suggested that pheromone-baited funnel traps were not useful for predicting mortality of pines nearby (Hayes et al. 2009). Conversely, pheromone trap catch of spruce beetle (*Dendroctonus rufipennis*) provided reliable estimates of Engelmann spruce mortality around the trap, albeit with large variance (Hansen et al. 2006; Negrón and Popp 2018).

Relationships between pheromone trap catch and indicators of population size were found to be more reliable for several Lepidoptera species. For example, catches of eastern spruce budworm (*Choristoneura fumiferana*, Tortricidae) by traps baited with sex pheromone showed a strong relationship with densities of spruce budworm larvae in the following year, which allowed prediction of outbreaks in eastern Canada up to six years in advance (Sanders 1988). However, at high population densities, trap catch was less indicative of population trends. Nevertheless, pheromone traps have been used for decades to monitor spruce budworm populations. Pheromone trap catch of the Nantucket pine tip moth (*Rhyacionia frustrana*, Tortricidae) in Georgia was moderately to highly correlated with population density and damage for the first adult generation but less so for subsequent generations within a year (Asaro and Berisford 2001). In France, pheromone trapping of the pine processionary moth was developed for population monitoring (Jactel et al. 2006) and tested from 2010 to 2016 across 50 pine plantations. This showed that trap catch is highly correlated with the annual number of attacked trees and can be used to predict infestations in the following year. Pheromone trap catch of a close relative, the oak processionary moth (*Thaumetopoea processionea*, Thaumetopoeidae), was less well correlated with local population densities in the U.K. (Straw et al. 2019). Nevertheless, the presence of nests within 250 m from a trap was successfully determined in 91% of cases.

Several important points need to be taken into consideration when evaluating relationships between trap catch and other indicators of insect presence, abundance, and damage: (i) traps can capture insects that have flown tens or hundreds of meters from where they had been feeding on a tree so that trap catch is not necessarily related to populations in the immediate neighborhood of a trap; (ii) insect populations can be highly patchy in space (Safranyik et al. 2004) and small numbers of traps may not provide an accurate indication of larger-scale abundance or damage, but a larger number of traps deployed at a site may do so (Schroeder 2013); (iii) when local populations are large, pheromone traps "compete" with many natural pheromone sources, and the same applies to traps baited with host plant volatiles when these are located in areas with an abundance of naturally occurring host plant volatiles (Wermelinger 2004; Schroeder 2013); (iv) the relationship between trap catch and population size may or may not be relevant depending on whether the purpose of trapping is for prediction of damage or just for detection of the presence of a species (as in pest detection and delimitation surveys) (Brockerhoff et al. 2013). Consequently, the choice of trapping or an alternative method depends on the purpose of

the activity. If prediction of population size is important, then a larger number of traps across a forest may be needed to obtain a better estimate and other factors such as the amount of host trees and the condition of sites need to be considered (Schroeder 2013). Furthermore, conclusions or inferences from trap catch data strongly depend on context such as catches of the same insect species in previous years or in traps at other locations in the same year.

19.4.2 Pheromone Trap Attraction Range

Beyond the intrinsic capture efficiency of an attractant-baited trap, it is important to know its attraction range, the area around a trap over which the target species is drawn towards the trap. The attraction range is relevant for validating correlations between trap catch and local population level at the same spatial scale. It is important for making inferences about the effective sampling area, i.e. the portion of the landscape where the target species can be detected, especially for surveillance of alien invasive pests (Kriticos et al. 2007). Additionally, knowledge of when the interception zones of adjacent traps overlap assists with designing pheromone trap networks (Manoukis et al. 2014) to optimize trap density, save time and reduce costs of trapping programs.

A common and convenient method of estimating the attraction range is based on analyzing interference between adjacent attractant-baited traps, considering that competition for insect capture would occur if two neighboring traps are sufficiently close to have overlapping attraction ranges (i.e. are at a distance shorter than twice their attraction range) (Schlyter 1992). To evaluate the distance between adjacent pheromone traps that would minimize competition and thus approximate the attraction range (or radius), a number of studies have been conducted with more or less complex grids, circles or groups of traps (Wall and Perry 1987; Schlyter et al. 1987; Elkinton and Cardé 1988; Oehlschlager et al. 2003; Jactel et al. 2019). Although the attraction range of pheromone traps for forest insects can vary greatly depending on trap design and the rate of release of pheromone lures, it is typically in the order of a few tens to hundreds of meters.

19.5 Other Detection Techniques Including Detector Dogs, E-Noses, Acoustic Detection and Molecular Techniques

19.5.1 Detection of Volatiles Emitted by Target Species

Most insects have a particular smell that may be related to pheromone production, some other biochemical process or other organisms associated with them. This can be exploited for surveillance purposes either by using chemical detection devices or with

trained dogs. In several countries, trained detector dogs (or 'sniffer dogs') are used at airports to detect imports infested with insects or to find smuggled or prohibited goods (USDA 2012). However, detector dogs can also be used in urban areas and in plant nurseries to detect trees or plants for planting that are infested by an unwanted insect. In Austria and other countries in Europe, dogs have been trained to detect *Anoplophora* beetles in wood packaging material, live plant imports, and in urban or rural areas (Hoyer-Tomiczek and Sauseng 2013). Such dogs can be very effective; for example, 15,000 plants imported from Asia were screened over a period of three days, and the dogs detected five plants that were infested by citrus longhorned beetle (*Anoplophora chinensis*, Cerambycidae) (Hoyer-Tomiczek and Sauseng 2013). In the US, an *Anoplophora* dog detection program was found to be 80–90% successful in detecting infested trees (Errico 2013). However, detector dogs are mainly suitable for particular target species; their use for generic detection of insects and fungi is limited due to the ubiquitous presence of these organisms.

Conventional analytical identification of volatile organic compounds (VOCs) can also be used for surveillance purposes. Typically, this involves headspace analysis by gas chromatography (GC) and mass spectrometry to characterize the volatiles associated with a target species. Once identified, the environment can be screened for these volatiles using a similar procedure. For example, volatiles emitted by the brown marmorated stinkbug (*Halyomorpha halys*, Pentatomidae) in a confined space were identified in this way, and it was then tested whether detectable concentrations of these volatiles could be isolated in a larger environment (Nixon et al. 2018). However, the highly diluted volatiles proved difficult to detect, and the sensitivity of this technique may rarely be sufficient for practical application in the field.

Another potentially suitable approach for detecting volatiles of target species is the use of electronic noses (e-noses). Proof-of concept studies have demonstrated the potential suitability of bio-electronic noses for detection purposes, but no such devices are ready for application on an operational basis, although considerable progress has been achieved (e.g. Oh et al. 2011; Du et al. 2013). It is expected that such devices will be available for practical use sometime in the 2020s (Glatz and Bailey-Hill 2011).

19.5.2 Acoustic Detection

Many insects produce sounds or vibrations for communication or in conjunction with movement or feeding (e.g. Hill 2008; Mankin et al. 2011). These acoustic and vibrational signals can be detected with a variety of sensors and devices, most of which are portable (Mankin et al. 2011). A key advantage of this technique is that it allows the detection of species that are hidden from sight such as wood borers and bark beetles inside wood, and it is non-destructive. As many species produce characteristic sounds, it may be possible to identify the type of organism or even the species by acoustic analysis (Bedoya et al. 2021). This technique has its limitations, though, as these signals are often very quiet and sensors need to be very close to the

source, and background noise can be a problem (Mankin et al. 2011). For example, the detection of bark beetle chirps under the bark of trees or logs is only possible within a distance of less than one meter and preferably much closer (Bedoya et al. 2022). Although operational application has been limited so far, acoustic detection of the red palm weevil (*Rhynchophorus ferrugineus*, Curculionidae), an invasive pest of palms that feeds inside palm trees is possible with a mobile acoustic detection system with > 80% accuracy (Herrick and Mankin 2012). Acoustic and low-frequency vibrational signals can also be detected with laser vibrometers. A portable laser vibrometer can be used to detect Asian longhorned beetles infesting trees or logs (Zorović and Čokl 2015).

19.5.3 Molecular Techniques and eDNA

Molecular techniques are increasingly used in a monitoring and surveillance context to identify insects. Eggs, larvae and pupae, which are difficult to identify using morphological characters, can often be identified with DNA barcoding using the mitochondrial COI gene (Frewin et al. 2013; Madden et al. 2019). There are also a wide range of molecular tools that are suitable for the detection and diagnosis of potentially invasive organisms on infested imports. These commonly use polymerase chain reaction (PCR) amplification in the laboratory but mobile PCR-based or loop-mediated isothermal amplification (LAMP) devices that can be used in the field are now available (Arif et al. 2013; Baldi and La Porta 2020), although these are used much more for pathogens than for insects. However, the use of environmental DNA (eDNA) has been shown to be effective in revealing the presence of small populations of invasive insects that may be difficult to detect with other methods (Valentin et al. 2018). Analysis by eDNA techniques of samples of plant material or rain water run-off on tree trunks could be a useful approach for surveillance and early detection of known target species.

19.6 Aerial Surveys and Remote Sensing

19.6.1 Aerial Surveys

When surveys are required for very large areas and ground-based surveillance and trapping programs are not practical, aerial surveys are often used. In North America, for example, aerial overview surveys of forest lands have been one of the foundations of forest pest management for decades (Hall et al. 2016). Aerial surveys are critical for assessing pest impacts in remote areas as well as for insects that impact forests at the landscape level. Yearly identification and mapping of numerous forest insect pests such as eastern spruce budworm, southern pine beetle, Douglas-fir

tussock moth (*Orgyia pseudotsugata*, Erebidae) and mountain pine beetle (*Dendroctonus ponderosae*, Scolytinae), provide assessments of infestations on forest lands (Aukema et al. 2006; Bouchard et al. 2006; Taylor and MacLean 2008; Hall et al. 2016). Aerial surveys can be affected by weather conditions and navigation but they are relatively accurate. For example, a comparison of aerial sketch mapping of annual defoliation by eastern spruce budworm and defoliation assessments on the ground showed that 85% of aerial mapping correctly classified defoliation as either nil to light (0–30%) or moderate to severe (31–100%) (Taylor and MacLean 2008). Apart from assessing current impacts, these data can be analyzed together with data on historical outbreak patterns to predict spatiotemporal patterns of future epidemics (see Aukema et al. 2006 for an example on mountain pine beetle).

Considerable effort goes into aerial forest health surveys. For example, in British Columbia, aerial overview surveys in 2019 were conducted for 80% of the province with 658 flight hours logged over 129 flight days (Westfall et al. 2019a). These revealed that a total of 5.9 million ha of forested lands were damaged by ≥ 46 agents (biotic and abiotic). Combined with directed ground inspections, these identified major infestations of 15 insect species and 10 diseases in coniferous forests while deciduous forests recorded impacts from 6 insect species and 2 diseases. Areas damaged by insects were greatest for the western balsam bark beetle in coniferous stands (3.2 million ha) and the aspen leaf miner in hardwood stands (1.3 million ha). Linking the incidences and expansions of tree mortality and defoliation with inventory databases permits accurate determinations of tree mortality and potential losses from such infestations, thereby broadly guiding management efforts such as stand thinning, sanitation and salvage logging, and insecticide applications.

Typically, aerial surveys are conducted by trained professionals per specific guidelines (see Westfall et al. 2019b, for example, for British Columbia). Surveyors identify tree species and damage agents from small planes or helicopters, sketch mapping types of damage and boundaries of disturbances directly on forest cover maps. The use of GIS and GPS has greatly improved the accuracy of aerial surveys. The use of aerial photography and remote sensing (see below) adds additional overlays to maps. Ground truthing of infestations is an important step to verify the accuracy of aerial surveys. In addition to species identification of causal agents, ground truthing can provide important information on the stage of infestations. In pine stands attacked by the mountain pine beetle, forest health professionals can assess attack densities on trees and the ratio of trees currently under attack to those that were attacked the previous year, providing a measure of risk for further attacks the following year. Integrating such data with inventory data on susceptible volumes of trees in the area helps determine the likelihood of further expansion of infestations.

Ground truthing can also help prevent over-reactions to apparent insect damage by forest managers. For example, sawflies can cause extensive defoliation on hemlocks in coastal forests of British Columbia (Nealis and Turnquist 2010). The visibility of red foliage over thousands of hectares can cause concern with forest managers resulting in initial impulses to log the area before timber is degraded by disease or checking. Ground truthing provides the opportunity to document that damage occurs on old foliage while new, current year foliage is untouched by sawflies. Moreover,

sawfly infestations are generally short-lived due to the effects of natural enemies. Examinations of branches in the field can readily verify high rates of parasitism of sawfly pupae. The use of drones or unmanned aerial vehicles (UAVs) with cameras can add significant benefits to ground truthing efforts, enabling surveyors the chance to examine crowns of tall trees and survey expansive regeneration stands that are difficult to traverse in person. Potential UAV applications are covered in the following section.

19.6.2   Remote Sensing of Forest Insect Damage

The use of remote sensing for forest health monitoring has increased substantially in recent years as research progress has made this an increasingly accessible and potentially powerful tool. Remote sensing involves high-resolution multi-spectral imagery acquired by satellites, aircraft or UAVs, which is processed (e.g. corrected for topography and atmospheric conditions) and analyzed (Hall et al. 2016; Stone and Mohammed 2017; Torresan et al. 2017). Satellite imagery can be of sufficient spatial resolution to enable identification of individual tree crowns or even individual branches, although there is a trade-off between resolution and the area displayed (i.e. the high-resolution 1.2-m pixel size of the Worldview-3 satellite sensor has an image width of only 13 km whereas the Landsat-8 satellite sensor has an image width of 185 km but a pixel size of 30 m, too coarse to display individual tree crowns) (Hall et al. 2016). Optical remote sensing captures the reflection of sunlight from trees and other structures, and the more separate spectral bands are recorded by a sensor, the better the spectral resolution and visualization of symptoms. The detection of insect damage is typically done by identifying damage-specific changes in spectral reflectance between images recorded from the same location in successive years, although a single image may sometimes suffice. The detection of change can be automated and there are many different approaches for doing this (Hall et al. 2016).

A review of uses of satellite imagery for detection of forest insect damage in North America has been compiled by Hall et al. (2016), including some 50 examples for mountain pine beetle, spruce beetle, eastern spruce budworm, western spruce budworm (*Choristoneura occidentalis*, Tortricidae), jack pine budworm (*Choristoneura pinus*, Tortricidae), spongy moth, and others. However, the uptake for operational use of satellite-based remote sensing data for forest health surveys has been limited so far. This has been attributed to several complicating factors including the requirement for species-specific spectral identification of insect damage, the limited time window when damage can be detected and atmospheric conditions/cloud cover need to be suitable, and difficulty with damage classification which typically occurs on a continuum rather than in specific classes (such as light, moderate, and severe) (Hall et al. 2016).

Despite some challenges, there is rapid progress with image resolution and analysis, and it can be expected that this technology will be adopted increasingly for operational use. When insect damage is sufficiently severe and detectable in satellite

images, then this methodology is already relatively powerful. For example, a study in Sweden investigated the onset of infestations of Norway spruce by the invading Hungarian spruce scale insect (*Physokermes inopinatus*, Coccidae) which causes characteristic black 'sooty mold' on the foliage (Olsson et al. 2012). Using SPOT satellite data, 78% of damage was detected successfully, and retrospective data analysis was able to identify the year when this characteristic damage first occurred (Olsson et al. 2012). One way in which damage symptoms can be identified with greater reliability is by combining data from passive light sensors with data from active systems like LiDAR (Light Detection and Ranging) and Radar sensors (Stone and Mohammed 2017).

Multispectral analysis of aerial imagery taken by aircraft uses the same principles as that of satellite imagery but it has the advantage of user-controlled timing of image acquisition when symptoms and atmospheric conditions are ideal. However, taking images by manned aircraft can become expensive when larger areas need to be surveyed. Using UAVs for this purpose is increasingly feasible and may be more cost-effective than using larger manned aircraft, especially when surveys involve smaller areas. Torresan et al. (2017) reviewed several studies that tested UAVs equipped with visible and near-infrared or hyperspectral cameras to detect and classify forest insect damage. The use of UAVs for this purpose was promising with a detection reliability of ca. 75–90%. A UAV remote sensing application for detecting bark beetle damage on individual urban trees was developed by Näsi et al. (2018) with similar levels of accuracy of identification of healthy, infested, and dead trees.

19.7 Outlook

The need for monitoring and surveillance of forest insects is likely to grow in importance. Insect outbreaks appear to become more frequent and more severe as multiple disturbance factors including climate change and other anthropogenic impacts disturb forest ecosystems. Likewise, international trade is expected to increase and involve ever more trading partners around the world, which will facilitate more arrivals and establishments of non-native species, despite our efforts to curb these. To keep up with these trends, early detection of both incursions of non-native species and outbreaks of native species will be critical to enable effective responses.

There is a large pool of methods for monitoring and surveillance and more are becoming available with the rapid progress of science and technology. Conventional methods such as surveillance of forests and high-risk sites by trained experts as well as trapping using targeted and broad-spectrum attractants will remain important. Trapping programs are likely to become more effective for a wider range of species as new attractants are being developed. Nevertheless, many species will remain for which trapping is not an option. A disadvantage of these conventional methods is their limited spatial coverage.

Several new technologies are being developed or refined that enable monitoring and surveillance over larger areas including enhanced aerial surveillance and remote

sensing using a variety of platforms. Progress with big data analysis and modelling also plays a role here. New developments in acoustic, chemical, and molecular detection methods and tools are also playing an increasingly important role. For example, the use of eDNA is promising for a range of surveillance applications. However, many of these methods are costly, and large-scale implementation would require large budgets. Conversely, better education and raised awareness among the wider public would be valuable without necessarily being costly. Citizen science projects are emerging in many countries and this is a promising development.

References

Allison D, Pike KS (1988) An inexpensive suction trap and its use in an aphid monitoring network. J Agr Entomol 5(2):103–107

Allison JD, Redak RA (2017) The impact of trap type and design features on survey and detection of bark and woodboring beetles and their associates: a review and meta-analysis. Annu Rev Entomol 62:127–146

Alvarez G, Gallego D, Hall DR, Jactel H, Pajares JA (2016) Combining pheromone and kairomones for effective trapping of the pine sawyer beetle *Monochamus galloprovincialis*. J Appl Entomol 140(1–2):58–71

Arif M, Fletcher J, Marek SM, Melcher U, Ochoa-Corona FM (2013) Development of a rapid, sensitive, and field-deployable razor ex biodetection system and quantitative PCR assay for detection of *Phymatotrichopsis omnivora* using multiple gene targets. Appl Environ Microbiol 79(7):2312–2320

Asaro C, Berisford CW (2001) Predicting infestation levels of the Nantucket pine tip moth (Lepidoptera: Tortricidae) using pheromone traps. Environ Entomol 30(4):776–784

Augustin S, Boonham N, De Kogel WJ, Donner P, Faccoli M, Lees DC, ... Roques A (2012) A review of pest surveillance techniques for detecting quarantine pests in Europe. EPPO Bull 42(3):515–551

Aukema BH, Carroll AL, Zhu J, Raffa KF, Sickley TA, Taylor SW (2006) Landscape level analysis of T pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography 29(3):427–441

Bakke A, Froyen P, Skattebol L (1977) Field response to a new pheromonal compound isolated from *Ips typographus*. Naturwissenschaften 64:98–99

Baldi P, La Porta N (2020) Molecular approaches for low-cost point-of-care pathogen detection in agriculture and forestry. Front Plant Sci 11:570862

Batista ES, Redak RA, Busoli AC, Camargo MB, Allison JD (2018) Trapping for *Sirex* woodwasp in Brazilian pine plantations: lure, trap type and height of deployment. J Insect Behav 31(2):210–221

Bedoya CL, Hofstetter RW, Nelson XJ, Hayes M, Miller DR, Brockerhoff EG (2021) Sound production in bark and ambrosia beetles. Bioacoustics 30(1):58–73

Bedoya CL, Nelson XJ, Brockerhoff EG, Pawson S, Hayes M (2022) Experimental characterization and automatic identification of stridulatory sounds inside wood. Roy Soc Open Sci 9: 220217. https://doi.org/10.1098/rsos.220217

Billings RF (2011) Aerial detection, ground evaluation, and monitoring of the southern pine beetle: state perspectives. In: Coulson RN, Klepzig KD (eds) Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. US Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, pp 245–246

Bloem K, Brockerhoff EG, Mastro V, Simmons GS, Sivinski J, Suckling DM (2014) Insect eradication and containment of invasive alien species. In: Gordh G, McKirdy S (eds) The handbook of plant biosecurity. Springer, Dordrecht, pp 417–446

Bouchard M, Kneeshaw D, Bergeron Y (2006) Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. Ecology 87(9):2319–2329

Branco M, Nunes P, Roques A, Fernandes MR, Orazio C, Jactel H (2019) Urban trees facilitate the establishment of non-native forest insects. NeoBiota 52:25–46

Bridges JR (1995) Exotic pests: major threats to forest health. In Eskew LG, comp. Forest Health Through Silviculture: Proceedings of the 1995 National Silviculture Workshop, Mescalero, New Mexico, May 8–11, 1995. Gen. Tech. Rep. RM-GTR-267. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp 105–113

Brockerhoff EG, Jones DC, Kimberley MO, Suckling DM, Donaldson T (2006) Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps baited with pheromones and kairomones. For Ecol Manag 228:234–240

Brockerhoff EG, Liebhold AM, Richardson B, Suckling DM (2010) Eradication of invasive forest insects: concepts, methods, costs and benefits. New Zealand J For Sci 40(Supplement):S117–S135

Brockerhoff EG, Suckling, DM, Kimberley M, Richardson B, Coker G, Gous S, ... Zhang A (2012) Aerial application of pheromones for mating disruption of an invasive moth as a potential eradication tool. PLoS ONE 7(8):e43767

Brockerhoff EG, Suckling DM, Roques A, Jactel H, Branco M, Twidle AM, ... and Kimberley MO (2013) Improving the efficiency of lepidopteran pest detection and surveillance: constraints and opportunities for multiple-species trapping. J Chem Ecol 39(1):50–58

Bulman LS (2008) Pest detection surveys on high-risk sites in New Zealand. Aust For 71(3):242–244

Byers JA (1989) Chemical ecology of bark beetles. Experientia 45:271–283

Campbell SA, Borden JH (2009) Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. Oikos 118:553–563

Carnegie AJ, Eldridge RH, Waterson DG (2005) History and management of *Sirex* wood wasp in pine plantations in New South Wales Australia. New Zealand J For Sci 35(1):3–24

CFIA [Canadian Food Inspection Agency] (2017) Brown spruce longhorn beetle—*Tetropium fuscum.* Retrieved July 2017, http://www.inspection.gc.ca/plants/plant-pests-invasive-species/insects/brown-spruce-longhorn-beetle/eng/1330656129493/1330656721978

Chase KD, Stringer LD, Butler RC, Liebhold AM, Miller DR, Shearer PW, Brockerhoff EG (2018) Multiple-lure surveillance trapping for *Ips* bark beetles, *Monochamus* longhorn beetles, and *Halyomorpha halys* (Hemiptera: Pentatomidae). J Econ Entomol 111(5):2255–2263

Clarke S (2012) Implications of population phases on the integrated pest management of the Southern pine beetle, *Dendroctonus frontalis.* J Integ Pest Manag 3:F1–F7

Colunga-Garcia M, Haack RA, Magarey RD, Borchert DM (2013) Understanding trade pathways to target biosecurity surveillance. NeoBiota 18:103–118

Czokajlo D, Ross D, Kirsch P (2001) Intercept panel trap, a novel trap for monitoring forest Coleoptera. J For Sci 47:63–65

de Groot P, Nott RW (2001) Evaluation of traps of six different designs to capture pine sawyer beetles (Coleoptera: Cerambycidae). Agr For Entomol 3:107–111

Dodds KJ (2014) Effects of trap height on captures of arboreal insects in pine stands of Northeastern United States of America. Can Entomol 146(1):80–89

Dodds KJ, Allison JD, Miller DR, Hanavan RP, Sweeney J (2015) Considering species richness and rarity when selecting optimal survey traps: comparisons of semiochemical baited flight intercept traps for Cerambycidae in Eastern North America. Agr For Entomol 17(1):36–47

Du L, Wu C, Liu Q, Huang L, Wang P (2013) Recent advances in olfactory receptor-based biosensors. Biosens Bioelectron 42:570–580

Ehler LE (2006) Integrated pest management (IPM): definition, historical development and implementation, and the other IPM. Pest Manag Sci 62(9):787–789

Einhorn J, Menassieu P, Michelot D, Riom J (1983) The use of sex-traps baited with synthetic attractants against the pine processionary, *Thaumetopoea pityocampa* Schiff. (Lep., Notodontidae) First Experiments in South-Western France. Agronomie 3:499–505

Elkinton JS, Cardé RT (1988) Effects of intertrap distance and wind direction on the interaction of gypsy moth (Lepidoptera: Lymantriidae) pheromone-baited traps. Environ Entomol 17(5):764–769

El-Sayed AM (2020) The Pherobase: database of pheromones and semiochemicals. https://www.pherobase.com

Epanchin-Niell RS, Brockerhoff EG, Kean JM, Turner JA (2014) Designing cost-efficient surveillance for early detection and control of multiple biological invaders. Ecol Appl 24(6):1258–1274

Errico M (2013) Asian longhorned beetle detector dog pilot project. In: McManus KA, Gottschalk KW (eds) Proceedings of the 23rd US Department of Agriculture Interagency Research Forum on Invasive Species 2012. General Technical Report NRS-P-114. United States Department of Agriculture Forest Service Northern Research Station, p 18

Faccoli M, Stergulc F (2006) A practical method for predicting the short-time trend of bivoltine populations of *Ips typographus* (L.) (Col., Scolytidae). J Appl Entomol 130(1):61–66

Fan JT, Denux O, Courtin C, Bernard A, Javal M, Millar JG, ... Roques A (2019) Multi-component blends for trapping native and exotic longhorn beetles at potential points-of-entry and in forests. J Pest Sci 92(1):281–297

Fernández Ajó AA, Martínez AS, Villacide JM, Corley JC (2015) Behavioural response of the woodwasp *Sirex noctilio* to volatile emissions of its fungal symbiont. J Appl Entomol 139(9):654–659

Ferro ML, Carlton CE (2011) A practical emergence chamber for collecting Coleoptera from rotting wood, with a review of emergence chamber designs to collect saproxylic insects. Coleopts Bull 65:115–124

Flaherty L, Gutowski JMG, Hughes C, Mayo P, Mokrzycki T, Pohl G, ... Sweeney J (2019) Pheromone-enhanced lure blends and multiple trap heights improve detection of bark and wood-boring beetles potentially moved in solid wood packaging. J Pest Sci 92(1):309–325

Frewin A, Scott-Dupree C, Hanner R (2013) DNA barcoding for plant protection: applications and summary of available data for arthropod pests. CAB Rev 8:18

Froud PM, Oliver TM, Bingham PC, Flynn AR, Rowswell NJ (2008) Passive surveillance of new exotic pests and diseases in New Zealand. In: Froud KJ, Popay AI, Zydenbos SM (eds) Surveillance for biosecurity: pre-border to pest management. New Zealand Plant Protection Society. https://nzpps.org/_oldsite/books/2008_Surveillance/Surveillance.pdf

Gery C, Miller C (1985) Evaluation of the populations of pine processionary caterpillar (*Thaumetopoea pityocampa* Schiff. Lepidopterae-Thaumetopoeidae) in Mont Ventoux, France. Annu For Sci 42:143–183

Glatz R, Bailey-Hill K (2011) Mimicking nature's noses: From receptor deorphaning to olfactory biosensing. Prog Neurobiol 93(2):270–296

Goodwin JT, Pawlowski SP, Mayo PD, Silk PJ, Sweeney JD, Hillier NK (2020) Influence of trap colour, type, deployment height, and a host volatile on monitoring *Orchestes fagi* (Coleoptera: Curculionidae) in Nova Scotia Canada. Can Entomol 152(1):98–109

Graham EE, Mitchell RF, Reagel PF, Barbour JD, Millar JG, Hanks LM (2010) Treating panel traps with a fluoropolymer enhances their efficiency in capturing cerambycid beetles. J Econ Entomol 103(3):641–647

Gries G, Gries R, Khaskin G, Slessor KN, Grant GG, Liška J, Kapitola P (1996) Specificity of nun and gypsy moth sexual communication through multiple-component pheromone blends. Naturwissenschaften 83(8):382–385

Haack RA (2006) Exotic bark-and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36(2):269–288

Haack RA, Rabaglia RJ (2013) Exotic bark and ambrosia beetles in the USA: potential and current invaders. In: Pena J (ed) Potential invasive pests of agricultural crop species. Wallingford, UK, CAB International, pp 48–74

Haack RA, Hérard F, Sun J, Turgeon JJ (2010) Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. Annu Rev Entomol 55:521–546

Häuser CL, Riede K (2015) Field methods for inventorying insects. In: Watson MF, Lyal C, Pendry C (eds) Descriptive taxonomy: the foundation of biodiversity research. Cambridge University Press, Cambridge, pp 190–213

Hall RJ, Castilla G, White JC, Cooke BJ, Skakun RS (2016) Remote sensing of forest pest damage: a review and lessons learned from a Canadian perspective. Can Entomol 148(S1):S296–S356

Hanks LM, Millar JG (2016) Sex and aggregation-sex pheromones of cerambycid beetles: basic science and practical applications. J Chem Ecol 42(7):631–654

Hansen EM, Bentz BJ, Munson AS, Vandygriff JC, Turner DL (2006) Evaluation of funnel traps for estimating tree mortality and associated population phase of spruce beetle in Utah. Can J For Res 36(10):2574–2584

Harris JWE, Collis DG, Magar KM (1972) Evaluation of the tree-beating method for sampling defoliating forest insects. Can Entomol 104(5):723–729

Hayes CJ, Fettig CJ, Merrill LD (2009) Evaluation of multiple funnel traps and stand characteristics for estimating western pine beetle-caused tree mortality. J Econ Entomol 102(6):2170–2182

Herrick NJ, Mankin RW (2012) Acoustical detection of early instar *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in Canary Island date palm, *Phoenix canariensis* (Arecales: Arecaceae). Fla Entomol 95(4):983–990

Hester SM, Cacho OJ (2017) The contribution of passive surveillance to invasive species management. Biol Invas 19(3):737–748

Hill PS (2008) Vibrational communication in animals. Harvard University Press, Boston

Howse P, Stevens JM, Jones OT (1998) Insect pheromones and their use in pest management. Chapman and Hall, London

Hoyer-Tomiczek U, Sauseng G (2013) Sniffer dogs to find *Anoplophora* spp. infested plants. J Entomol Acarol Res 45:10–12

Jacquet JS, Orazio C, Jactel H (2012) Defoliation by processionary moth significantly reduces tree growth: a quantitative review. Annu For Sci 69(8):857–866

Jacquet JS, Bosc A, O'Grady A, Jactel H (2014) Combined effects of defoliation and water stress on pine growth and non-structural carbohydrates. Tree Physiol 34(4):367–376

Jactel H, Menassieu P, Vétillard F, Barthélémy B, Piou D, Frérot B, ... Battisti A (2006) Population monitoring of the pine processionary moth (Lepidoptera: Thaumetopoeidae) with pheromone-baited traps. For Ecol Manag 235:96–106

Jactel H, Bonifacio L, Van Halder I, Vétillard F, Robinet C, David G (2019) A novel, easy method for estimating pheromone trap attraction range: application to the pine sawyer beetle *Monochamus galloprovincialis*. Agr For Entomol 21(1):8–14

Kalaris T, Fieselmann D, Magarey R, Colunga-Garcia M, Roda A, Hardie D, ... Whittle P (2014) The role of surveillance methods and technologies in plant biosecurity. In: Gordh G, McKirdy S (eds), The handbook of plant biosecurity. Dordrecht, Springer, pp 309–337

Kean JM, Suckling DM, Sullivan NJ, Tobin PC, Stringer LD, Smith GR, Kimber B, Lee DC, Flores Vargas R, Fletcher J, Macbeth F, McCullough DG, Herms DA, et al (2020) Global eradication and response database. http://b3.net.nz/gerda (accessed 29 July 2020)

Kerr JL, Kelly D, Bader MKF, Brockerhoff EG (2017) Olfactory cues, visual cues, and semiochemical diversity interact during host location by invasive forest beetles. J Chem Ecol 43(1):17–25

Knuff AK, Winiger N, Klein AM, Segelbacher G, Staab M (2019) Optimizing sampling of flying insects using a modified window trap. Methods Ecol Evol 10(10):1820–1825

Kriticos DJ, Potter KJ, Alexander NS, Gibb AR, Suckling DM (2007) Using a pheromone lure survey to establish the native and potential distribution of an invasive Lepidopteran *Uraba Lugens*. J Appl Ecol 44(4):853–863

Lantschner MV, Corley JC (2015) Spatial pattern of attacks of the invasive woodwasp *Sirex noctilio*, at landscape and stand scales. PLoS ONE 10(5):e0127099

Li S, Daudin JJ, Piou D, Robinet C, Jactel H (2015) Periodicity and synchrony of pine processionary moth outbreaks in France. For Ecol Manag 354:309–317

Liebhold A, Thorpe K, Ghent J, Lyons DB (1994) Gypsy moth egg mass sampling for decision-making: a users' guide. USDA Forest Service Northeastern Area, Forest Health Protection, Report NA-TP-04-94

Liebhold AM, Brockerhoff EG, Garrett LJ, Parke JL, Britton KO (2012) Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Front Ecol Environ 10(3):135–143

Liebhold AM, Berec L, Brockerhoff EG, Epanchin-Niell RS, Hastings A, Herms DA, ... Yamanaka T (2016) Eradication of invading insect populations: from concepts to applications. Annu Rev Entomol 61:335–352

Liebhold AM, Kean JM (2018) Eradication and containment of non-native forest insects: successes and failures. J Pest Sci 92:83–91

Lindelöw Å, Schroeder M (2001) Spruce bark beetle, *Ips typographus* (L.), in Sweden: monitoring and risk assessment. J For Sci 47:40–42

Lindgren BS (1983) A multiple funnel trap for scolytid beetles (Coleoptera). Can Entomol 115(3):299–302

Löfstedt C, Wahlberg N, Millar JG (2016) Evolutionary patterns of pheromone diversity in Lepidoptera. In: Allison JD, Cardé RT (eds) Pheromone communication in moths: evolution, behavior and application. University of California Press, pp 43–82

Madden MJ, Young RG, Brown JW, Miller SE, Frewin AJ, Hanner RH (2019) Using DNA barcoding to improve invasive pest identification at US ports-of-entry. PLoS ONE 14(9):e0222291

Mankin RW, Hagstrum DW, Smith MT, Roda AL, Kairo MT (2011) Perspective and promise: a century of insect acoustic detection and monitoring. American Entomol 57(1):30–44

Manoukis NC, Hall B, Geib SM (2014) A computer model of insect traps in a landscape. Sci Rep UK 4:7015

Mayfield AE, III, Salom SM, Sumpter K, McAvoy T, Schneeberger NF, Rhea R (2020) Integrating chemical and biological control of the hemlock Woolly Adelgid: a resource manager's guide. FHAAST-2018–04. USDA Forest Service, Forest Health Assessment and Applied Sciences Team, Morgantown, West Virginia

Miller DR, Rabaglia RJ (2009) Ethanol and (−)-α-pinene: attractant kairomones for bark and ambrosia beetles in the Southeastern US. J Chem Ecol 35(4):435–448

Miller DR, Dodds KJ, Eglitis A, Fettig CJ, Hofstetter RW, Langor DW, Mayfield AE III, Munson AS, Poland TM, Raffa KF (2013) Trap lure blend of pine volatiles and bark beetle pheromones for Monochamus spp. (Coleoptera: Cerambycidae) in pine forests of Canada and the United States. J Econ Entomol 106:1684–1692

Miller DR, Crowe CM, Dodds KJ, Galligan LD, de Groot P, Hoebeke ER, Mayfield AE III, Poland TM, Raffa KF, Sweeney JD (2015) Ipsenol, ipsdienol, ethanol and α-pinene: Trap lure blend for Cerambycidae and Buprestidae (Coleoptera) in pine forests of Eastern North America. J Econ Entomol 108:1837–1851

Miller DR, Allison JD, Crowe CM, Dickinson DM, Eglitis A, Hofstetter RW, Munson AS, Poland TM, Reid LS, Steed BE, Sweeney JD (2016) Pine sawyers (Coleoptera: Cerambycidae) attracted to α-pinene, monochamol, and ipsenol in North America. J Econ Entomol 109:1205–1214

Miller DR, Crowe CM, Mayo P, Silk PJ, Sweeney JD (2017) Interactions between ethanol, syn-2,3-hexanediol, 3-hydroxyhexan-2-one, and 3-hydroxyoctan-2-one lures on trap catches of hardwood longhorn beetles in Southeastern United States. J Econ Entomol 110:2119–2128

Millar JG, Hanks LM (2017) Chemical ecology of cerambycids. In: Wang Q (ed) Cerambycidae of the world: biology and pest management. CRC Press, Boca Raton, London, New York, pp 161–208

Morris RF (1960) Sampling insect populations. Annu Rev Entomol 5(1):243–264

Muirhead-Thompson RC (1991) Trap responses of flying insects: the influence of trap design on capture efficiency. UK, Academic Press, London

Näsi R, Honkavaara E, Blomqvist M, Lyytikäinen-Saarenmaa P, Hakala T, Viljanen N, ... Holopainen M (2018) Remote sensing of bark beetle damage in urban forests at individual tree level using a novel hyperspectral camera from UAV and aircraft. Urban For Urban Green 30:72–83

Nealis VG, Turnquist R (2010) Impact and recovery of Western hemlock following disturbances by forestry and insect defoliation. For Ecol Manag 260(5):699–706

Negrón JF, Popp JB (2018) Can spruce beetle (*Dendroctonus rufipennis* Kirky) pheromone trap catches or stand conditions predict engelmann spruce (*Picea engelmannii* Parry ex Engelm.) tree mortality in Colorado? Agr For Entomol 20(2):162–169

Nixon LJ, Morrison WR, Rice KB, Brockerhoff EG, Leskey TC, Guzman F, ... Rostás M (2018) Identification of volatiles released by diapausing brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae). PLoS ONE 13(1):e0191223

Oehlschlager AC, Leal WS, Gonzalez L, Chacon M, Andrade R (2003) Trapping of *Phyllophaga elenans* with a female-produced pheromone. J Chem Ecol 29(1):27–36

Oh EH, Song HS, Park TH (2011) Recent advances in electronic and bioelectronic noses and their biomedical applications. Enzyme Microb Technol 48(6):427–437

O'Leary K, Hurley JE, MacKay W, Sweeney J (2003) Radial growth rate and susceptibility of *Picea rubens* Sarg. to *Tetropium fuscum* (Fabr.). In: McManus ML, Liebhold AM (eds) Proceedings: ecology, survey, and management of forest insects; 2002 September 1–5; Krakow, Poland. Gen.Tech. Rep. NE-311, U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA, pp 107–114. https://www.fs.usda.gov/treesearch/pubs/download/6071.pdf

Olsson PO, Jönsson AM, Eklundh L (2012) A new invasive insect in Sweden-*Physokermes inopinatus*: tracing forest damage with satellite based remote sensing. For Ecol Manag 285:29–37

Pawson SM, Sullivan JJ, Grant A (2020) Expanding general surveillance of invasive species by integrating citizens as both observers and identifiers. J Pest Sci 93:1155–1166. www.findapest.nz

Poland TM, Petrice TR, Ciaramitaro TM (2019) Trap designs, colors, and lures for emerald ash borer detection. Front Forests Global Change 2:80

Poland TM, Rassati D (2019) Improved biosecurity surveillance of non-native forest insects: a review of current methods. J Pest Sci 92(1):37–49

Post KE, Werner RA (1988) Wood borer distribution and damage in decked white spruce logs. Northern J Appl Forest 5:49–51

Prasad Y, Prabhakar M (2012) Pest monitoring and forecasting. In: Abrol D, Shankar U (eds) Integrated pest management: principles and practice. CABI, Oxfordshire, UK, pp 41–57

Quilici S, Donner P, Battisti A (2012) Surveillance techniques for non-native insect pest detection. EPPO Bull 42(1):95–101

Rabaglia R, Duerr D, Acciavatti R, Ragenovich I (2008) Early detection and rapid response for non-native bark and ambrosia beetles: summary of the 2001–2005 pilot project. USDA Forest Service, Forest Health Protection

Rabaglia RJ, Cognato AI, Hoebeke ER, Johnson CW, LaBonte JR, Carter ME, Vlach JJ (2019) Early detection and rapid response: a 10-year summary of the USDA forest service program of surveillance for non-native bark and ambrosia beetles. American Entomol 65(1):29–42

Rassati D, Marini L, Marchioro M, Rapuzzi P, Magnani RG, Poloni R, Di Giovanni F, Mayo P, Sweeney J (2019) Developing trapping protocols for wood-boring beetles associated with broadleaf trees. J Pest Sci 92:267–279

Ravlin FW (1991) Development of monitoring and decision-support systems for integrated pest management of forest defoliators in North America. Forest Ecol Manag 39:3–13

Reding ME, Schultz PB, Ranger CM, Oliver JB (2011) Optimizing ethanol-baited traps for monitoring damaging ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) in ornamental nurseries. J Econ Entomol 104(6):2017–2024

Redlich S, Clemens J, Bader MKF, Pendrigh D, Perret-Gentil A, Godsoe W, ... Brockerhoff EG (2019) Identifying new associations between invasive aphids and pinaceae trees using plant sentinels in botanic gardens. Biol Invas 21(1):217–228

Roques A (ed) (2015) Processionary moths and climate change: an update. Springer, Dordrecht

Ryall K, Silk P, Webster RP, Gutowski JM, Meng Q, Li Y, Gao W, Fidgen J, Kimoto T, Scarr T, Mastro V, Sweeney JD (2015) Further evidence that monochamol is attractive to *Monochamus* (Coleoptera: Cerambycidae) species, with attraction synergized by host plant volatiles and bark beetle (Coleoptera: Curculionidae) pheromones. Can Entomol 147:564–579

Safranyik L, Shore TL, Linton DA (2004) Measuring trap efficiency for bark beetles (Col., Scolytidae). J Appl Entomol 128(5):337–341

Sanders CJ (1988) Monitoring spruce budworm population density with sex pheromone traps. Can Entomol 120(2):175–183

Schlyter F (1992) Sampling range, attraction range, and effective attraction radius: estimates of trap efficiency and communication distance in coleopteran pheromone and host attractant systems 1. J Appl Entomol 114(1–5):439–454

Schlyter F, Byers JA, Löfqvist J (1987) Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. J Chem Ecol 13(6):1503–1523

Schroeder LM (2013) Monitoring of *Ips typographus* and *Pityogenes chalcographus*: influence of trapping site and surrounding landscape on catches. Agr Forest Entomol 15(2):113–119

Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D, ... and Linsenmair KE (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574:671–674

Sharov AA, Leonard D, Liebhold AM, Roberts EA, Dickerson W (2002) "Slow the spread" a national program to contain the gypsy moth. J Forest 100:30–36

Silk P, Sweeney J, Wu J, Price J, Gutowski J, Kettela E (2007) Evidence for a male produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). Naturwissenschaften 94:697–701

Slippers B, Hurley BP, Wingfield MJ (2015) *Sirex* woodwasp: a model for evolving management paradigms of invasive forest pests. Annu Rev Entomol 60:601–619

Smith G, Hurley JE (2000) First North American record of the Palearctic species *Tetropium fuscum* (Fabricius) (Coleoptera: Cerambcyidae). Coleopts Bull 54:540

Stevens PM (2008) High risk site surveillance (HRSS): an example of best practice plant pest surveillance. In: Froud KJ, Popay AI, Zydenbos SM (eds) Surveillance for biosecurity: pre-border to pest management. New Zealand Plant Protection Society, pp 127–134. https://nzpps.org/_oldsite/books/2008_Surveillance/Surveillance.pdf

Stone C, Mohammed C (2017) Application of remote sensing technologies for assessing planted forests damaged by insect pests and fungal pathogens: a review. Curr For Rep 3(2):75–92

Straw NA, Hoppit A, Branson J (2019) The relationship between pheromone trap catch and local population density of the oak processionary moth *Thaumetopoea processionea* (Lepidoptera: Thaumetopoeidae). Agr Forest Entomol 21(4):424–430

Sukovata L, Dziuk A, Parratt M, Bystrowski C, Dainton K, Polaszek A, Moore R (2020) The importance of trap type, trap colour and capture liquid for catching *Dendrolimus pini* and their impact on by-catch of beneficial insects. Agr For Entomol 22(4):319–327

Sweeney J, de Groot P, MacDonald L, Smith S, Cocquempot C, Kenis M, Gutowski J (2004) Host volatile attractants and traps for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* (L.), and other longhorned beetles (Coleoptera: Cerambycidae). Environ Entomol 33:844–854

Sweeney J, Gutowski J, Price J, de Groot P (2006) Effect of semiochemical release rate, killing agent, and trap design on capture of *Tetropium fuscum* (F.), and other longhorn beetles (Coleoptera: Cerambycidae). Environ Entomol 35:645–654

Sweeney J, Hughes C, Webster V, Kostanowicz C, Webster R, Mayo P, Allison JD (2020) Impact of horizontal edge–interior and vertical canopy–understory gradients on the abundance and diversity of bark and woodboring beetles in survey traps. Insects 11(9):573

Taylor SL, MacLean DA (2008) Validation of spruce budworm outbreak history developed from aerial sketch mapping of defoliation in New Brunswick. Northern J Appl Forest 25(3):139–145

Tobin PC, Blackburn LM (eds) (2007) Slow the spread: a national program to manage the gypsy moth. Gen. Tech. Rep. NRS-6. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA

Tobin PC, Kean JM, Suckling DM, McCullough DG, Herms DA, Stringer LD (2014) Determinants of successful eradication programs. Biol Invas 16:401–414

Toïgo M, Barraquand F, Barnagaud JY, Piou D, Jactel H (2017) Geographical variation in climatic drivers of the pine processionary moth population dynamics. Forest Ecol Manag 404:141–155

Torresan C, Berton A, Carotenuto F, Di Gennaro SF, Gioli B, Matese A, ... Wallace L (2017) Forestry applications of UAVs in Europe: a review. Int J Remote Sens 38(8-10):2427–2447

USDA [United States Department of Agriculture] (2012) National detector dog manual. United States Department of Agriculture APHIS PPQ report, p 262. http://www.aphis.usda.gov/import_export/plants/manuals/ports/downloads/detector_dog.pdf

USDA [United States Department of Agriculture] (2019) Gypsy moth program manual. United States Department of Agriculture, Washington DC. https://www.aphis.usda.gov/import_export/plants/manuals/domestic/downloads/gypsy_moth.pdf

Valentin RE, Fonseca DM, Nielsen AL, Leskey TC, Lockwood JL (2018) Early detection of invasive exotic insect infestations using eDNA from crop surfaces. Front Ecol Environ 16(5):265–270

Vega JM, Moneo I, Ortiz JCG, Palla PS, Sanchís ME, Vega J, ... Roques A (2011) Prevalence of cutaneous reactions to the pine processionary moth (Thaumetopoea pityocampa) in an adult population. Contact Dermat 64(4):220–228

Wall C, Perry JN (1987) Range of action of moth sex-attractant sources. Entomol Exp Appl 44(1):5–14

Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. Forest Ecol Manag 202(1–3):67–82

Westfall J, Ebata T, Bains B (2019a) Summary of forest health conditions in British Columbia. Pest Management Report Number 15. Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Victoria, British Columbia. https://www2.gov.bc.ca/assets/gov/environment/research-monitoring-and-reporting/monitoring/aerial-overview-survey-documents/aos_2019a.pdf

Westfall J, Ebata T, HR GISolutions Inc (2019b) Forest health aerial overview survey standards for British Columbia. Ministry of Forests, Lands, Natural Resource Operations and Rural Development, Victoria, British Columbia. https://www.for.gov.bc.ca/ftp/HFP/external/!publish/Aerial_Overview/Data_stds/AOS%20Standards%202019b.pdf

Wichmann L, Ravn HP (2001) The spread of *Ips typographus* (L.) (Coleoptera, Scolytidae) attacks following heavy windthrow in Denmark, analysed using GIS. Forest Ecol Manag 148(1–3):31–39

Wild Spotter (2020) *Wild spotter—mapping invasives in America's wild places.* University of Georgia, USA, www.wildspotter.org

Zorović M, Čokl A (2015) Laser vibrometry as a diagnostic tool for detecting wood-boring beetle larvae. J Pest Sci 88(1):107–112

Chapter 20
Silviculture

Kristen M. Waring and Ethan Bucholz

20.1 Introduction

Silviculture is the art and science of managing forest stands to meet landowner goals and objectives (see Box 20.1); traditional examples of goals and objectives include managing for timber production, improved wildlife habitat, fuels reduction, and maintenance or improvement of forest health. Within forest health, objectives often involve mitigating negative impacts of forest insects while recognizing the beneficial role of insects in provision of ecosystem services. Goals tend to be broad, encompassing perspective on desired conditions at large scales, such as the forest or landscape. Objectives are more specific, and often target specific outcomes (e.g. reduced levels of insect-caused mortality following treatment) and are typically focused at the stand-scale. In this chapter, we have focused on the stand-scale unless explicitly noted otherwise. Silviculture, through prescriptions and treatment implementation (see Box 20.1 for definitions) can be used to manipulate the species composition, vertical and horizontal structure of the stand, individual and stand-level tree vigor, and numerous other stand characteristics that might influence susceptibility to insects. Numerous silvicultural treatments exist (e.g. prescribed fire); however, mechanical removal of trees is perhaps the most common association people make with silvicultural treatments to meet management objectives. The outcomes targeted by silvicultural prescriptions will depend upon the site, existing stand characteristics, specific insect(s) of concern, and any other management objectives.

K. M. Waring (✉) · E. Bucholz
Northern Arizona University, Flagstaff, AZ, USA
e-mail: Kristen.Waring@nau.edu

E. Bucholz
Colorado State Forest Service, Fort Collins, CO, USA

Box 20.1: Silviculture definitions used in this chapter. From *The Dictionary of Forestry* (Helms 1998) unless otherwise indicated

Term	Definition
Silviculture	The art and science of controlling the establishment, growth, composition, health, and quality of forests and woodlands to meet the diverse needs and values of landowners and society on a sustainable basis
Silviculture Prescription	A planned series of treatments designed to change current stand structure to one that meets management goals
Silvicultural Treatment	A management intervention conducted to achieve desired goals (definition by authors)
Stand	A contiguous group of trees sufficiently uniform in age-class distribution, composition and structure and growing on a site of sufficiently uniform quality to be a distinguishable unit
Even-aged stand	A stand of trees composed of a single age class
Uneven-aged stand	A stand of trees of three or more distinct age classes, either intimately mixed or in small groupings
Multi-aged stand	A stand of trees with two or more distinct age classes
Regeneration	Seedlings or saplings existing in a stand
Residual tree(s)	A tree or snag remaining after an intermediate or partial cutting of a stand
Stand density	A quantitative measure of stocking expressed either absolutely in terms of number of trees, basal area, or volume per unit area or relative to some standard condition
Stand development	Changes in forest stand structure over time
Stand structure	The horizontal and vertical distribution of components of a forest stand including the height, diameter, crown layers, and stems of trees, shrubs, herbaceous understory, snags, and down woody debris
Intermediate treatment	Any treatment or tending designed to enhance growth, quality, vigor and composition of the stand after establishment or regeneration and prior to final harvest

(continued)

(continued)

Term	Definition
Thinning	An intermediate treatment made to reduce stand density of trees primarily to improve growth, enhance forest health, or recover potential mortality. Variations on the most common types of thinning (defined below) are common • Low thinning: removal of trees in the suppressed/overtopped crown class in order to favor those in the upper crown classes. *Syn thin from below* • Mechanical thinning: thinning of trees involving removal of trees in rows, strips or by using fixed spacing intervals. *Syn geometric thinning* • Crown thinning: removal of trees from the dominant or co-dominant crown classes in order to favor the best trees of those same crown classes • Dominant thinning: removal of trees in the dominant crown class in order to favor the lower crown classes. *Syn selection thinning; thin from above*
Sanitation cutting	The removal of trees to improve stand health by stopping or reducing the actual or anticipated spread of insects and disease
Salvage cutting	The removal of dead trees or trees damaged or dying because of injurious agents other than competition, to recover economic value that would otherwise be lost
Regeneration method	A cutting procedure by which a new age class is created. Traditional methods are: • Clearcut: the cutting of essentially all trees, producing a fully exposed microclimate for the development of a new age class • Coppice: All trees from the previous stand are cut and the majority of regeneration is from sprouts or root suckers. *Syn. clearfell* • Seed tree: the cutting of all trees except for a small number of widely dispersed trees retained for seed production and to produce a new age class in fully exposed microenvironments • Shelterwood: the cutting of most trees, leaving those needed to produce sufficient shade to produce a new age class in a moderated environment. Modifications are numerous, and include group shelterwood with non-uniform spacing of residual trees post-harvest and shelterwoods with reserves, in which the residual trees are not removed, creating a two-aged stand • Group Selection: trees are removed and new age classes are established in small groups • Single tree selection: individual trees of all size classes are removed more or less uniformly throughout the stand, to promote growth of remaining trees and to provide space for regeneration

The goals of this chapter are:

1. To identify broad approaches and specific silvicultural strategies and tools managers can use to alleviate or prevent forest insect problems such as mortality or reduced growth and vigor; and
2. To discuss the impact of silvicultural strategies and tools on forest structure, stand development, and other biotic and abiotic factors as well as forest insect population dynamics.

20.2 Silvicultural Strategies for Management of Forest Insects

From a silvicultural perspective, managing forest insects can be considered in two broad approaches: (1) those that increase resistance, and/or (2) those that increase resilience (DeRose and Long 2014; Table 20.1). Resistance is the ability of a system to withstand change; that is, a resistant forest stand will have the same condition, structure, and species composition before and after a disturbance (Walker et al. 2004). Resilience is the ability of a system to change but maintain its basic attributes; a resilient forest stand subjected to disturbance will return to conditions similar to those present prior to the disturbance but may have changes in structure (Walker et al. 2004). A more entomological perspective would place silvicultural strategies into the categories of reducing susceptibility or vulnerability along with increasing regeneration potential (Muzika and Liebhold 2000). This chapter takes the silvicultural perspective in terminology, but the underlying theoretical basis for treatments between the two perspectives is highly compatible.

Strategies designed to increase stand resistance focus on the influence of structure and species composition on the potential severity of a given insect disturbance (DeRose and Long 2014). Severity is principally determined by how much mortality or die-back is associated with an insect outbreak. Strategies to increase stand resilience are longer-term and focus on how the disturbance influences stand structure and species composition (DeRose and Long 2014). Silviculture can be used in both approaches to mitigate anticipated negative impacts, with prescriptions based on characteristics of, and predictions for, individual stands.

Resistance and resilience strategies can be applied separately or as complementary short- and long-term treatments to ensure that live trees remain in a stand over longer time horizons. For example, the spruce beetle (*Dendroctonus rufipennis*) in the western United States tends to target mature overstory spruce (*Picea* spp.) and may cause extensive mortality in stands dominated by large spruce (>90%) (DeRose and Long 2007, and references therein). In the short-term, reducing overstory density may increase resistance of existing trees to spruce beetle attack, thus maintaining similar stand conditions by preventing extensive overstory mortality. Over a longer time period, resilience is necessary to maintain healthy stand conditions. Windmuller-Campione and Long (2015) defined resilience of spruce-fir stands to spruce beetle

Table 20.1 Approaches to increasing resistance and resilience using silvicultural strategies to adjust vertical and horizontal stand structure, their impact on residual trees and potential impact on bark beetle and defoliator damage. Assumes species composition is not altered during treatment. See Box 20.1 for definitions

Broad approach	Silvicultural strategy	Residual vertical structure	Residual horizontal structure	Impact for bark beetle hazard	Impact for defoliator damage
Intermediate silvicultural operations					
Resistance	Thinning from below/geometric thinning/Low intensity prescribed fire	Simple: one canopy layer	Regular	Increases tree size, vigor and phloem thickness/may increase susceptibility if trees were low vigor prior to treatment	Reduces complexity of vertical structure, decreasing dispersal through canopy; faster tree recovery at lower tree densities
Resistance	Thinning from above/crown thinning	Simple: one canopy layer	Regular, assuming even distribution of lower canopy classes in stand	Decreases tree size; tree vigor and phloem thickness decrease or remain unchanged	May leave small suppressed trees susceptible to dispersal from residual overstory trees (if present); faster tree recovery at lower tree densities
Resistance or resilience	Variable density thinning/free thinning	Dependent upon pre-treatment structure; generally won't change vertical structure	Patchy, with openings and dense areas across stand	Increases tree size, vigor and phloem thickness in patches; denser areas have no change in susceptibility	No change due to vertical canopy structure remaining the same; patches not large enough to prevent dispersal onto regeneration; faster tree recovery at lower tree densities

(continued)

Table 20.1 (continued)

Broad approach	Silvicultural strategy	Residual vertical structure	Residual horizontal structure	Impact for bark beetle hazard	Impact for defoliator damage
	Regeneration methods				
Resistance	Clearcut/traditional shelterwood/seed tree	Simple: one canopy layer	Dependent upon regeneration methods and patterns	Immediate decrease; will increase with time since treatment as trees age and grow larger	Immediate decrease if shelterwood or seed trees are removed within 10 years; small clearcuts will be susceptible to re-infestation from neighboring stands
Resilience	Group shelterwood or shelterwood with reserves[a]	2 canopy layers (shelterwood with reserves)	Patchy	Overstory trees remain susceptible if clumped (lower vigor) and if left in the stand	Increases susceptibility of new cohort to dispersal from overstory
Resilience	Single tree and Group selection	Multiple canopy layers	Patchy but can be regular within groups if group selection	Varies by canopy layer, tree size, and whether increased tree vigor is greater than insect pressure on large trees with thick phloem	High susceptibility of dispersal to all canopy layers which may be lessened at low residual densities; groups not large enough to prevent dispersal to regeneration; faster tree recovery at lower tree densities

[a] also applies to clearcut or seed tree with reserves

outbreaks as adequate stocking of Engelmann spruce (*Picea engelmannii*) regeneration following an outbreak. Resilience is provided through the use of young spruce to replace overstory spruce trees lost during the outbreak, providing for live trees in the stand over a long time period. Silviculture can be used proactively (prior to an outbreak) to create conditions conducive to Engelmann spruce regeneration, thus increasing long-term resilience.

Silvicultural treatments are also commonly categorized according to whether they target direct or indirect control of forest insects, primarily in bark beetle management (Fettig et al. 2014). Direct control strategies are meant to immediately reduce current insect populations. Indirect strategies focus on proactive management meant to reduce the potential for future tree damage. Most silvicultural strategies are indirect and consequently the primary focus of this chapter. However, a few common direct control tools are identified where appropriate.

20.2.1 Structural Strategies

Silvicultural strategies that adjust the vertical or horizontal stand structure can target both increased resistance or resilience at the stand-scale. Such strategies attempt to reduce the potential for large-scale insect infestations and can include a number of silvicultural treatments that result in a wide range of vertical and horizontal stand structures. Adjustments to vertical and horizontal stand structure can be effective because some stand structures are more susceptible to damage from forest insect pests. Silviculture can be used to shift stand structures from more susceptible to less susceptible states. Susceptible stand structures vary depending upon the insect pest species, corresponding tree host species characteristics and underlying site conditions.

Two common guilds of forest insect pests are bark beetles (see Chapter 10, Bark Beetles) and foliage feeders (defoliators; see Chapter 9, Foliage Feeders). Susceptible forest structures associated with damage by some of the most damaging agents within these guilds can be quite different, leading to trade-offs between structures: a structure that creates resistance or resilience to a bark beetle may lessen these attributes when considering a defoliator, for example. It is important to understand the mechanisms driving these relationships and why shifting structures can be an effective management strategy.

Bark beetles need to successfully find host trees and overcome tree defenses; they also require bark with thick enough phloem to complete their development and ensure reproductive success. Some bark beetle species require relatively large trees as hosts (e.g. mountain pine beetle (*Dendroctonus ponderosae*) in lodgepole pine (*Pinus contorta*)) while other bark beetle species need smaller diameters to successfully complete their life cycle (e.g. pine engraver (*Ips pini*) in ponderosa pine (*Pinus ponderosa*)). Defoliators need to find appropriate host trees, but some species are limited to relatively short distance dispersal, often by wind and gravity from upper to lower crowns or trees, or by crawling between individual trees. Hence,

complex, multilayered vertical structures are more conducive to defoliator success than simple, single canopy layers. Conversely, bark beetle populations are favored by simple structures of even-sized trees.

Silvicultural treatments that remove trees alter stand structure immediately, and the indirect control of insect damage is based on changes to the microclimate within the stand and the ability for insects to find appropriate host trees. Microclimatic changes include disruption of the chemical signals used by insects to find host trees and mates (Progar et al. 2014) and changing individual tree microclimates enough to reduce the suitability of host trees (e.g. by creating warmer conditions along the tree bole). Microclimates within the stand may also be altered enough to affect insect success. For example, increased temperatures or insolation may result in increased mortality during the dispersal phase and/or the early larval stage. In order to reduce the ability of insects to find appropriate host trees, managers can reduce the number of host trees available, change the average tree size, and/or create a vertical or horizontal structure not conducive to successful host location by the insect (Fettig et al. 2014).

Tree vigor in general refers to the overall health of trees, and can be assessed qualitatively, by visually rating tree crowns (Miller and Keen 1960) or quantitatively, by comparing growth rates of trees to each other and their potential to succumb to insect attack. Quantitative assessments of tree vigor require additional field measurements, and may be assessed along with qualitative crown ratings, typically through the use of tree cores to measure annual or periodic basal area growth, sapwood area (water conducting tissue) and density or size of defensive structures (resin ducts) (Kane and Kolb 2010). While early research often related sapwood area to leaf area (photosynthetic capacity of the tree) to define vigor (Waring and Pitman 1980), other researchers have found a simple measure of basal area increment adequately captures individual tree vigor (defined by increased resin flow) (McDowell et al. 2007). Trees that produce less sapwood per unit leaf area typically require fewer bark beetle attacks for successful colonization (Waring and Pittman 1980) and Mitchell et al. (1983) related this to stand density, finding that reducing tree density was an effective method for increasing relative resistance to bark beetle attack by increasing tree growth per unit of leaf area. Ultimately, silviculture can shift stand structure to increase resistance and/or resilience, with the underlying cause of the increase likely a combination of multiple factors working together (Fig. 20.1).

Silvicultural treatments to reduce structural complexity include thinning from below and traditional even-aged regeneration methods (Table 20.1). Silvicultural strategies to reduce defoliation and its impacts have not been researched as thoroughly as strategies for bark beetle management and damage mitigation. The lack of empirical studies documenting post-treatment reductions in defoliation and/or defoliation damage means treatment effects are largely hypothetical, based on expected stand responses (Muzika and Liebhold 2000). Additionally, increasing tree vigor through density reduction may not alleviate defoliation severity, but may enable trees to recover more quickly following defoliation (Fajvan and Gottschalk 2012). A wide variety of traditional and modified silvicultural treatments are used to alter vertical and horizontal stand structure, many of which are identified, along with the
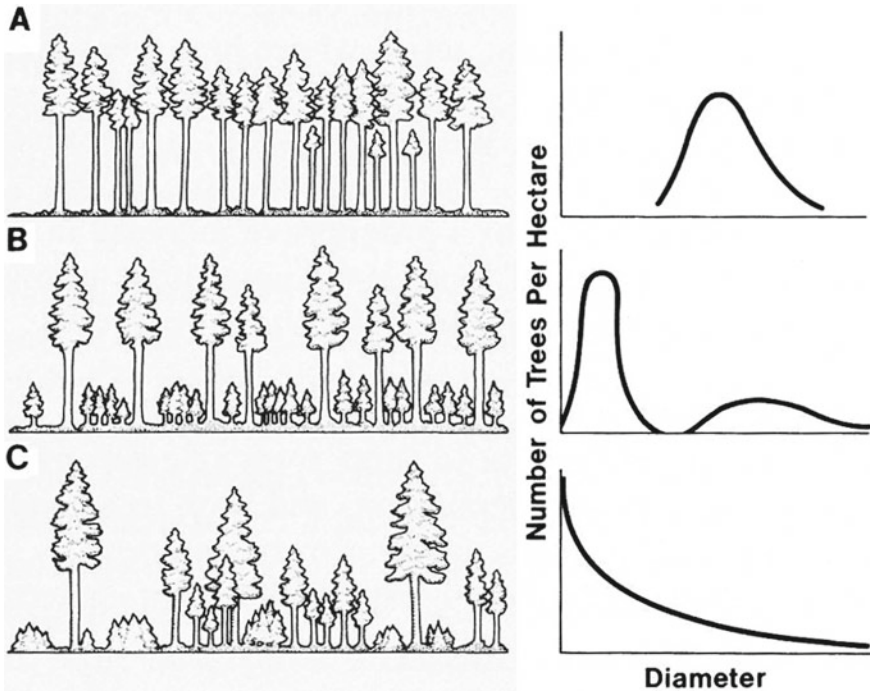
Fig. 20.1 Susceptibility to defoliation damage increases as structural complexity increases, from **A** through **C**. From Brookes et al. (1987)

anticipated impact of treatment on bark beetle and defoliator damage (Table 20.1). Additionally, each strategy is placed into either the resistance or resilience approach.

Traditional thinning results in a regular spatial pattern, creating similar spacing between residual trees. This pattern may be more resilient to bark beetle outbreaks from a tree vigor perspective, than leaving trees irregularly spaced where inter-tree competition remains high within groups of trees. However, inter-tree distance can also influence microclimate and negatively affect dispersal, and mate- and host-finding ability; a factor to consider when designing thinning regimes and spatial patterns of residual (leave) trees.

Much research has focused on the use of thinning to prevent bark beetle outbreaks in the United States, and the majority of research indicates that thinning can be effective at reducing tree mortality during outbreaks (i.e. thinned stands have less mortality than denser, unthinned stands) (Fettig et al. 2007). Dense, unthinned stands are generally considered to be at high hazard of bark beetle infestation and subsequent tree mortality, and hazard rating systems include metrics such as stand basal area or trees per unit area as an indicator variable. While thinning may reduce the probability of future mortality from bark beetles in most conifer species, some tree mortality should be expected when bark beetle populations rise to very high levels and pressure on the stand is high, except at low to moderate stand densities (15–20 m^2 ha^{-1})

(McGregor et al. 1987; Schmid and Mata 2005; Hansen et al. 2010). However, different bark beetle species, sites, and host species may have different thresholds. For example, stand susceptibility to southern pine beetle (*Dendroctonus frontalis*) decreases when stands are thinned to under $7.5 \, \mathrm{m}^2 \, \mathrm{ha}^{-1}$ basal area (Nowak et al. 2008 and references within, Nowak et al. 2015). Additionally, bark beetle mortality may create conditions more resilient to future outbreaks by increasing the proportion of unfavorable size classes or host species (Kashian et al. 2011). Ultimately, the reduction of stand density to a critical threshold that is site and species specific is more important than whether silviculture, bark beetles, or some other damaging agent causes the density reduction. In stands impacted by defoliators, thinning can improve the ability of defoliated trees to recover to previous rates of growth (Fajvan and Gottschalk 2012).

Regeneration methods fall into both the resistance and resilience categories given their effects on the overstory and understory over both short- and long-term time frames (Table 20.1). Most even- and uneven-aged regeneration methods reduce overstory density and stand susceptibility while providing for regeneration, which is not an objective of intermediate treatments, including thinning (see Box 20.1 for definitions). The exceptions are clearcuts, which reduce density to zero, do not increase vigor because no overstory trees remain, alter the microclimate dramatically, and provide for regeneration when implemented correctly. Traditional seed tree and shelterwood regeneration methods result in the same stand structure as a clearcut, and all three eliminate the potential for bark beetle-caused mortality until the newly regenerated trees reach a susceptible size.

Even-aged regeneration methods can be modified (e.g. group shelterwood or any even-aged system with reserves; Table 20.1) to provide additional structure by leaving residual overstory trees. These trees would have increased vigor and experience an altered microclimate, both factors which can influence bark beetle attacks. These methods result in two-aged or multi-aged stands (Table 20.1) and can also be resistant and resilient to bark beetle outbreaks. The large overstory trees will be at a low density and, depending on spatial pattern, spaced at a distance far enough from each other to reduce inter-tree competition and create conditions less conducive to successful insect mating, dispersal, and host-finding. Until the youngest age class reaches a susceptible size and density, extensive mortality from bark beetles is unlikely. Regeneration methods can also be used to enhance development of a new age class of trees, creating long-term resilience by providing for young trees if bark beetles kill the overstory (Windmuller-Campione and Long 2015). Group shelterwood methods may be useful in promoting such resilience in spruce stands dominated by large diameter, even-aged trees. These stands are highly susceptible to spruce beetle, which is a particularly aggressive bark beetle that may kill the entire overstory during an outbreak. Prior to an outbreak, implementing a group shelterwood to create conditions for a new spruce age class in the understory results in a stand that will have live trees, albeit young and small, following the outbreak (Windmuller-Campione and Long 2015).

Other insects less common than bark beetles and defoliators can also cause stand-scale damage. White pine weevils (*Pissodes stobi*) infest the leaders of seedlings,

resulting in multiple forks and stem deformities. White pine weevils are most abundant in open areas that promote higher temperatures in the understory and thicker leader diameters in seedlings (Ostry et al. 2010; Pitt et al. 2016). Group shelterwood or shelterwood with reserves methods (Table 20.1) that leave the residual trees intact can be used to successfully regenerate eastern white pine (*Pinus strobus*) while mitigating white pine weevil damage. The overstory cover provided through these systems (50–75% full sunlight or up to 26 m² ha⁻¹) provides enough cover to moderate the microclimate and reduce eastern white pine regeneration leader diameters, thus reducing damage from the white pine weevil (Stiell and Berry 1985; Pitt et al. 2016).

Multi-aged regeneration methods can result in structures that are both resistant and resilient to bark beetle outbreaks due to the vertical complexity that results (O'Hara 2014). However, resistance may vary across the stand, as a complex horizontal structure can also result in dense groups of trees that are competing heavily under a similar microclimate as pre-treatment. Such pockets of trees may remain susceptible to bark beetle attack. However, Kollenberg and O'Hara (1999) found multiaged stands tended to have higher leaf area indices and basal area increment compared to even-aged stands.

The benefits of structural complexity and the overall increased resistance and resilience are likely to outweigh the consequences of small-scale pockets of lower vigor trees. In uneven-aged, single-species stands, treatments that reduce density only marginally are not likely to alter the microclimate or tree vigor enough to reduce bark beetle hazard and may have the opposite effect. For example, a low thinning that removes only suppressed/overtopped trees increases average tree size—a factor that could increase bark beetle hazard. However, if the stand is being converted from a simple structure to a more complex structure, resistance and resilience will increase to bark beetles while decreasing to defoliators following harvest. The opposite would be expected if a stand is shifted from a more complex structure to a simplified vertical and / or horizontal structure. It therefore requires a careful balancing of objectives to arrive at a vertical and horizontal structure that is both resistant and resilient to bark beetles and defoliators while also meeting other objectives, such as timber production or fire hazard reduction. In the western United States, timber production is becoming less of a societal value and healthy forested landscapes resilient to large-scale mortality events that provide biodiversity and wildlife habitat are taking precedence. In these forests, reducing overall stand density to a low basal area (~35% of carrying capacity) has the potential to meet these new objectives without creating increased insect susceptibility or wildfire hazard.

Sanitation is an intermediate treatment and direct control approach used to reduce insect population levels in a stand (Box 20.1). The objective of sanitation treatment is to improve stand health by removing trees infested or likely to be infested by insects. Controlling a bark beetle population using sanitation is not considered a viable option, with the exception of the southern pine beetle. Spot infestations (Fig. 20.2) of southern pine beetle can be controlled, thus avoiding a landscape-scale outbreak, using either cut-and-remove or cut-and-leave strategies. If trees can

be removed and handled appropriately following removal from the site, cut-and-remove strategies are preferred (Fig. 20.3; Fettig et al. 2007). However, cut-and-leave strategies, in which cut trees are left onsite, can also be effective and do not appear to increase the hazard of attacks in nearby trees (Fettig et al. 2007 and references therein).

Southern pine beetle outbreaks have decreased in frequency since the 1950's despite a concomitant increase in the acreage of pine plantations. One hypothesis related to the decline in outbreaks is that intensive silviculture practices have resulted in less susceptible stands (lower density, higher average tree vigor) than were present in earlier decades (Asaro et al. 2017). Widespread use of sanitation strategies may also

Fig. 20.2 Spot infestation of southern pine beetle, from above (left) and below (right). Modified from Asaro et al. (2017)
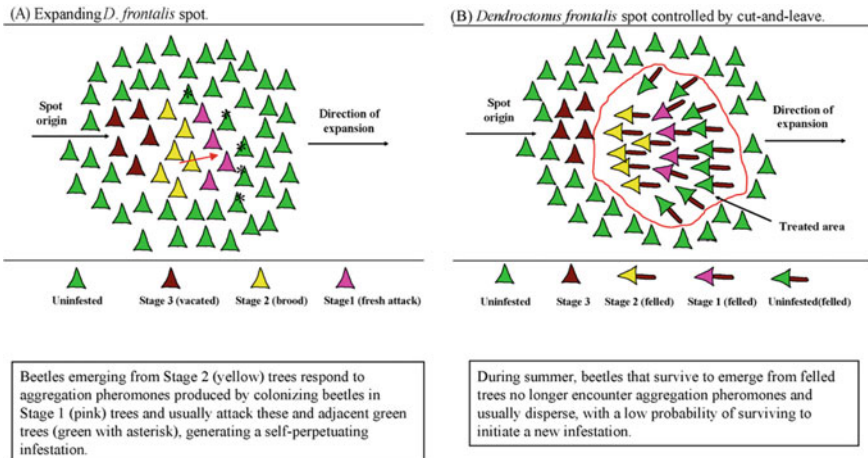

Fig. 20.3 Illustration of an expanding spot infestation (A) and the cut-and-leave sanitation treatment implemented to control southern pine beetle (B). From Fettig et al. (2007)

have a role in outbreak frequency reduction, as cut-and-remove and cut-and-leave strategies are implemented quickly in new spot infestations (Asaro et al. 2017).

Coniferous forests composed of a single species, size and age class will be highly susceptible to bark beetle outbreaks when these factors align with insect pest host preferences. When bark beetle populations are high, even trees in lower density stands may be attacked and overcome by beetles. In these situations, sanitation may be the best option if attacked and dead trees need to be removed. For example, dead trees in recreation areas are hazard trees and pose a safety threat to visitors and should be removed using a sanitation treatment. Numerous dead trees in more remote locations may not warrant removal if they do not pose a safety issue and recovering economic value from these trees is not an objective.

20.2.2 Strategies to Adjust Species Composition

Many forest insect pests are considered specialists, preferring specific tree host species over others. In some insects, this host preference is quite strong and attacks on non-preferred species are rare (e.g. spruce beetle). Other insects have a range of tree hosts, with one generally preferred over others but finding several species attacked in a stand would not be considered unusual. Bark beetles tend to have narrower host ranges than defoliators. Defoliators frequently infest a range of host species, with an order of preference. For example, western spruce budworm (*Choristoneura freemanii*) is an unfortunately named species, as it preferentially attacks true fir (*Abies* spp.). Infestation of spruce (*Picea* spp.) occurs, but damage and mortality may be less severe or occur after the true fir have been fully infested and are dead or declining from multiple, successive defoliation events (Polinko 2014; Vane et al. 2017). Western spruce budworm inhabits a wide geographic range across western North America, and preferentially feeds on tree hosts in order of tree shade tolerance patterns (Brookes et al. 1978). Other defoliators vary more in their host preferences; Douglas-fir tussock moth (*Orgyia pseudotsugata*) primarily feeds on white fir (*Abies concolor*) in the southwestern US, switching to a preference for either grand fir (*Abies grandis*) or Douglas-fir (*Pseudotsuga mensiezii*) in the northern Rocky Mountains, depending on site conditions, and even further north, in Canada's Rocky Mountains, feeds primarily on Douglas-fir (Brookes et al. 1985). However, even with changing geographic host tree preference (i.e. when a species' host tree preference differs throughout its range), preferred host tree species still exhibit higher shade tolerance than less preferred species in the same stand (e.g. pine species (*Pinus* spp.). Under certain circumstances, such as at high larval population levels or when non-preferred tree hosts are surrounded by more preferred tree hosts, feeding will occur on all tree species in the area. Defoliator damage to host trees ranges from short- and long-term growth reductions to widespread mortality following multiple, recurring defoliation events (Naidoo and Lechowicz 2001; Vane et al. 2017; Rapp 2017).

Silvicultural strategies designed to adjust species composition are primarily used to mitigate defoliator damage and mortality but could also be used to prevent or mitigate other insect infestations, particularly if tree host preference is known. Defoliators disperse from upper to lower tree canopies; the most susceptible stands are dense with a species composition composed primarily of the most preferred host species in multiple vertical canopy layers. Abiotic site factors, including warmer, drier sites that are more prone to drought (e.g. upper ridges), can also play a pre-disposing role in defoliator hazard. If one or more, less preferred host tree species are present or planned for after treatment, silviculture can be an effective indirect control method of reducing the potential for future insect damage. Intermediate treatments or regeneration methods can be used (Box 20.1, Table 20.1); the prescription should remove dead and dying infested trees and live trees of the most preferred tree host species. Such a prescription should also adjust the vertical and horizontal stand structure in a complementary manner to increase both resistance and resilience. Additionally, other stand objectives are typically accounted for in the prescription, including fire hazard reduction, timber production, and wildlife habitat.

Eastern spruce budworm (*Choristoneura fumiferana*) prefers balsam fir (*Abies balsmaea*) over white spruce (*Picea glauca*) and black spruce (*Picea mariana*) in eastern Canada, and also tends to cause the highest levels of mortality in dense mature balsam fir stands. A silvicultural prescription that both reduces density and preferentially removes mature balsam fir will result in a stand with a lower probability of future damage (DeGroot et al. 2005). Similar strategies are being implemented to reduce western spruce budworm damage in the southwestern US; the prescription reduces density to increase overall tree vigor and shifts species composition towards less preferred host trees such as quaking aspen (*Populus tremuloides*) and ponderosa pine. White fir and defoliated Douglas-fir are preferentially removed (Fig. 20.4). When developing silvicultural prescriptions, it is important to understand differences in the ecology of insect species. For example, while eastern spruce budworm causes mortality in mature balsam fir first, western spruce budworm mortality tends to occur first in the smaller size classes (Brookes et al. 1978; DeGroot et al. 2005).

Another opportunity to shift species composition occurs during the regeneration phase. Silviculture can be used to encourage certain species to naturally regenerate over others or artificial regeneration can be used to select a specific species composition and density for the new age class. Ensuring adequate natural regeneration can be challenging following widespread overstory mortality if live trees are not available to provide a seed source. In the case of defoliators, heavily defoliated live trees will often have limited capacity for seed production following defoliation (Brookes et al. 1978). In these stands, natural regeneration of less preferred host tree species is more likely than regeneration of the most susceptible host species. A shift toward less preferred host tree species can be encouraged even more by removing preferred host trees from the overstory and leaving only less preferred host trees to regenerate the stand. Such a composition shift may or may not be desirable, depending upon the objectives of the silvicultural treatment.

Planting is the best way to ensure regeneration by less preferred host trees. In most situations, complete replacement of preferred host tree species with less preferred

Fig. 20.4 Silviculture used to reduce western spruce budworm damage and mortality on the Kaibab National Forest, Arizona, USA. The treatment reduced stand density, created openings to promote regeneration, and favored less preferred host species as residual trees. Photo by K. Waring

host tree species will not be desirable, as this represents a stand conversion. Single-species plantations may also be vulnerable to a different suite of insect and/or disease problems but may be warranted to meet landowner goals and objectives, such as timber production. Generally, planting will entail a subtle shift from dominance by preferred host tree species to dominance by less preferred host tree species by planting a reduced density of the preferred tree host species.

20.2.3   Potential Drawbacks to the Use of Silviculture

It is possible to create conditions more conducive to insect damage and mortality through silviculture. For example, regenerating eastern white pine under full sun will lead to white pine weevil problems in certain regions (Ostry et al. 2010). It is the responsibility of the silviculturist to know and understand the silvics and ecology of the trees and their pests in a given stand to avoid creating these problems. Silviculturists frequently rely on forest health experts to provide information about specific, stand-level insect or disease issues that may be a concern before or after treatment. Pruning large live branches during bark beetle flight periods can result in attacks leading to mortality, thus pruning treatments should be timed to occur outside of these flight periods whenever possible. Generally, the objectives of pruning for wood quality will not create conditions conducive to bark beetle attack as the stands targeted for pruning treatments are young, and small live branch removal from conifers has not been found to increase bark beetle susceptibility. Hadfield and Flanagan (2000) found pruning increased susceptibility to Douglas-fir beetle attack in campgrounds where large live branches were pruned to meet a hazard tree objective (removal of dwarf mistletoe (*Arceuthobium douglasii*)-infected branches with large brooms).

Prescribed burning, even at low intensity and severity that does not outright kill the overstory trees, can increase susceptibility to bark beetle attacks through crown scorch and injuries to the cambium (McHugh et al. 2003; Billings et al. 2004). Post-fire tree mortality due to bark beetle attack tends to be short-term (Kane et al. 2017) but as we increase the use of prescribed fire as a management tool, caution is warranted (Bentz et al. 2009). Frequent use of prescribed fire also reduces stand resilience by removing tree regeneration. Central American forests were subject to management practices that reduced both resistance and resilience, resulting in a large, landscape-scale southern pine beetle outbreak (Billings et al. 2004).

The interactions between tree physiology (including tree defenses), herbivory, and abiotic stresses are complex and a review of these is beyond the scope of this chapter (see Massad and Dyer (2010) and Ryan et al. (2015) and literature cited within, for a review and overview of these concepts).

From a silvicultural perspective, thinning has the potential to not just increase tree vigor, but also increases residual tree growth, leading to thicker phloem. Very dense stands have small individual trees with thin phloem that limits bark beetle development and reproduction. Such stands may have reduced susceptibility to bark beetle attacks; thinning may increase susceptibility by increasing average tree size and phloem thickness (Anhold et al. 1996). Very low stand densities have historically been resistant to bark beetle attacks (as described previously in this chapter). Recent research indicates that individual trees in such stands may be less resilient to drought, possibly due to an inability to maintain large crowns when water is limiting (D'Amato et al. 2013).

Drought stress has been linked to increased insect activity in multiple tree species (Savage 1994; Gaylord et al. 2013; Anderegg et al. 2015; Kolb et al. 2016;). Very

low and very high stand densities may not be conducive to long-term resistance or resilience given this interaction. A recent study suggests that drought lowers tree resistance to infection by some bark beetle fungal symbionts (Klutsch et al. 2017). During drought conditions, stress is often manifested within individual trees as reduced growth (Fischer et al. 2010; Thomas and Waring 2015; Sohn et al. 2016).

The ability of individual trees within a stand to recover to pre-drought growth rates can be an indicator of susceptibility to bark beetles. Fischer et al. (2010) found that at high stand densities (~14 m^2 ha^{-1}) ponderosa pine trees that failed to return to pre-drought growth rates were preferentially attacked by the rounded pine beetle (*Dendroctonus adjunctus*). Douglas-fir tussock moth and western spruce budworm damage tends to be higher on sites more prone to drought conditions (Brookes et al. 1978, 1985). This effect is likely linked to the preferred host species being among the least drought tolerant at these sites. Thinning may also change the chemical composition of residual tree foliage, leading to increased susceptibility. In spruce-fir stands of northeastern North America, thinning altered the foliar monoterpene concentrations of both spruce and fir, making them more susceptible to defoliation from eastern spruce budworm (Fuentealba and Bauce 2011). Due to the complex interactions described above, the response to thinning is not always predictable, nor does it always lead to reductions in herbivory.

Implementing silvicultural treatments can result in logging damage to residual trees and increases slash on the forest floor. To avoid increasing residual tree susceptibility to bark beetle attack, logging operations should be timed to occur when bark beetle flights are low or not occurring, and care should be taken to avoid damaging live trees. Slash piles can serve as suitable host material for many *Ips* species, which may then 'spill-over' into the tops of neighboring trees (Kegley et al. 1997). Slash piles should be removed, chipped or burned in a timely manner to avoid this problem. Freshly cut logs and log decks of large trees can result in fast build-up of certain bark beetles as well (such as the spruce beetle), which then move on to attack live trees nearby (Reynolds and Holsten 1994). Logging activities may damage the soil, increasing compaction, erosion, and/or rutting. Soil damage can lead to increased tree stress, and susceptibility to insect damage, such as the Douglas-fir tussock moth (Brookes et al. 1978).

20.2.4 Linkages with Integrated Pest Management

As discussed in Chapter 17, Integrated Pest Management (IPM) is an integrated approach, which considers multiple strategies and tactics to manage pests efficiently while incorporating economic, social and ecological components. In forest entomology, IPM has primarily focused on efforts to reduce or describe more targeted approaches for land managers using insecticides, and silviculture adds another tool to help reduce potentially environmentally damaging chemical agents on the landscape (McIntire 1988).

It should be noted that silviculture is an IPM tactic. Generally considered cultural strategies, these tactics are generally defined as any treatment that involves a modification of established practices to make a host less favorable for pests or minimize the loss of a particular commodity. Concepts of preventative management are readily applicable to silvicultural strategies. In stands where pest outbreaks are a concern, using management tactics to foster resistance and/or resilience in the resulting stand is crucial (Table 20.1). Silvicultural tactics can be used in tandem with other management activities to increase resistance and/or resilience, while also providing opportunities for other, more immediate tactics to be implemented should pest populations increase. In this section, we cover the use of silviculture in combination with monitoring, chemical control, biological control, and genetic selection.

20.2.5   Silviculture and Monitoring

As discussed previously in Chapter 19, effective monitoring of insect activity is the critical first step of developing an appropriate IPM response. Monitoring should be conducted in a way that is both regular and economically feasible, in order to continually update information on insect population sizes and activity. Management actions should be based on regular assessments of both the insect pest population size and their potential to inflict damage. Conducting regular stand assessments for insect activity, in addition to more stationary and passive approaches, i.e. insect traps, should be both conducted annually, and monitored frequently, to best identify areas where insect activity is increasing. Land managers use this information to prioritize stands for management and abate potential large-scale insect damage or mortality.

Proactive management entails preparing unaffected areas such that if the problem occurs (i.e. non-native invasive expands its non-native range) stands are better able to cope with these changes (e.g. Schoettle and Sniezko 2007). Monitoring pest spread is a key component of proactive management facilitating the identification of high-risk areas (i.e. as characterized by stand conditions, species compositions, vertical/horizontal structure, edaphic and abiotic features of the landscape). Silvicultural actions triggered through monitoring demonstrate the potential of the combination of these two strategies to better prepare forested stands for potential or imminent pest expansion and movement.

In long-term forestry projects, regular monitoring is crucial to determine if silvicultural approaches are warranted (i.e. the identification of emerging threats). Post-treatment, they can be used to evaluate treatment impact on target pest populations. Favorable environmental conditions, or certain disturbances (wind-throw events, storm damage, etc.) can lead to rapid insect population growth. Regular monitoring facilitates the identification of both changes in insect populations and above-threshold population levels [levels above which severe economic damage occurs (see Chapter 19)], both of which are critical to maintaining the health and vigor of forest stands.

Monitoring is critical for effective management of non-native, invasive insects. For example, the sirex woodwasp (*Sirex noctilio*), an invasive insect of pines that recently established in northeastern North America (Hoebeke et al. 2005), the combined approach of proper silvicultural management and monitoring population expansion, whether through trapping or categorizing infestations aerially, helps land managers determine a proper course of action. Stand resistance to sirex woodwasp can be increased through thinning prior to insect invasion. Maintenance of both host tree vigor through basal area reductions (for eastern white and red (*Pinus resinosa*) pines these are reported between 9.3 and 14 m^2 ha^{-1}), creates stands that are optimal for tree growth and therefore production of defensive compounds (Gilmore and Palik 2006; Dodds et al. 2007). Monitoring allows managers to prioritize treatment of pre-invasion stands while considering location of those stands across the landscape.

Monitoring is also an important consideration for native insect pests. Bark beetles are especially damaging during epidemic population cycles. Due to their ubiquity in the Northern Hemisphere, methods such as aerial detection, trapping, ground surveys and remote sensing have been developed and implemented widely for monitoring, and newer technologies, such as unmanned aerial vehicles, are being considered (Wulder et al. 2005; Fettig and Hilszczanski 2015; Morris et al. 2017). Ultimately, proactive monitoring in combination with silvicultural strategies, such as direct control of potential infestations, can be effective preventative measures to make stands and landscapes less susceptible to widespread mortality from the activity of both non-native and native pests.

20.2.6 Silviculture and Chemical Control (Insecticides)

As discussed previously the impetus for the development of IPM was largely generated by an over-reliance on insecticides and the subsequent development of insecticide resistance. However, chemical control is still a large part of any IPM strategy, and proper timing of applications and insecticide selection can yield multiple benefits. For example, the North Carolina Department of Agriculture recommends spraying Fraser fir (*Abies fraseri*) plantations with a number of pyrethroid insecticides during specific times of the year to control for multiple pests such as balsam woolly adelgid (*Adelges piceae*), balsam twig aphid (*Mindarus abietinus*) and hemlock rust mite (*Nalepella tsugifoliae*) (Sidebottom 2009). The timing of the applications, coupled with adequate tree spacing in these plantation settings, highlights an effective IPM strategy combining silviculture (spacing, tree growth) with insecticide use. Pest populations are reduced when problematic, while minimizing the number of insecticide applications required to reach the management goal.

Effective and economical use of chemicals cannot always be achieved in forest settings. Chemical control is expensive and difficult to apply at landscape-scales or in remote areas, highlighting the necessity of having multiple management strategies to manage pests. Imidacloprid, a neonicotinoid systemic pesticide, has been used by the National Park Service to protect eastern hemlock (*Tsuga canadensis*) from damage

caused by the invasive insect, hemlock woolly adelgid (*Adelges tsugae*) in both trunk and soil applications (NPS Environmental Assessment 2007). Current research is showing that hemlock woolly adelgid responds negatively to increased light and that releasing these shade-tolerant species using silviculture (e.g. crown thinning, where eastern hemlock are the favored residual trees, with the objective of sustaining the species) may be a strategy to reduce pest populations through stand manipulations. This strategy may be particularly useful for releasing understory hemlock, especially in riparian areas and other areas not feasibly sprayed with insecticides (Brantley et al. 2017).

Carlson et al. (1983) suggest simplifying stand vertical structure (i.e. single-canopy or two-aged), and varying species composition are viable silvicultural strategies to mitigate damage and potential population increase of western spruce budworm in spruce-fir forests. By simplifying canopy strata/altering composition, land managers build natural barriers to population expansion on longer time scales, while using insecticides in untreated and susceptible stands. These examples highlight how insecticide use can be minimized by the creation of less susceptible stand conditions through active IPM management strategies.

Targeted insecticide use can reduce impacts on non-target species and can effectively reduce pest populations during outbreaks. When coupled with regeneration methods (Table 20.1), chemical control can be utilized to protect the future stand. For example, Gottschalk (1993) recommended shelterwood regeneration methods in stands vulnerable to spongy moth (*Lymantria dispar*), followed by aerial application of insecticides. This strategy reduces insect population numbers while building resilience through the regenerating trees. While chemical control may still be an effective management tool to reduce pest numbers during outbreaks, using silviculture to maintain tree vigor and maintain or enhance understory species diversity and abundance [as habitat for potential biological control agents (e.g. natural predators and parasitoids)], can provide useful components of IPM programs that help to alleviate the need for chemical control (Elek and Wardlaw 2013).

20.2.7 Semiochemicals

Chemical control also includes the use of semiochemicals, organic molecules produced by plants or animals that mediate behavioral interactions between organisms. Semiochemicals involved with intraspecific (within species) communication are pheromones, and those involved with interspecific (between species) communication are allelochemicals. Synthetic copies of these signals and cues can be used in monitoring and management programs for forest insects. For example, verbenone, an anti-aggregation pheromone released by both mountain pine beetle and western pine beetle (*Dendroctonus brevicomis*), has been utilized to directly protect many different species of western North American conifers (e.g. Gillette et al. 2012; Borden et al. 2006; Fettig and Munson 2020). Site factors such as lower stand densities and

higher temperatures diminish its efficacy on a stand-scale when deployed as individual slow-release packets (Fettig et al. 2009), while area-wide deployment on the forest floor in flake releasing formulations effectively reduce beetle mass-attacks on individuals (Gillette et al. 2014).

These strategies, referred to as push/pull strategies, exploit bark beetle behavior to repel pests from the desired resource (e.g. a stand or individual tree) and pull them towards a resource that can then be managed to explicitly eradicate attracted individuals (Cook et al. 2007). Push strategies use numerous tactics including but not limited to semiochemicals (both host- and pest-derived) such as anti-feedants (host-derived chemicals that deter insect feeding activities), anti-aggregants (such as verbenone) and alarm pheromones (pest-derived pheromones that elicit fight-or-flight responses) (Cook et al. 2007).

Push strategies emphasize keeping the pest away from resources (e.g. host trees), while pull strategies tend to use attractants to concentrate individuals in an area. Trap trees represent a common tactic used as a pull strategy in controlling endemic and epidemic bark beetle populations (e.g. Fettig et al. 2007). Felled trees, which mimic windthrown trees, are targeted by some species of bark beetle, therefore felling and baiting trap trees with an aggregation pheromone can be an effective pull strategy (e.g. Schmid and Frye 1977). Trap trees then need to be removed from the stand in a sanitation operation to limit population build-up in stands. Combined with silvicultural strategies such as harvesting infested individuals (as in sanitation treatments; Table 20.1), trap trees (both baited and non-baited) are effective at controlling endemic populations of beetles (e.g. Bentz and Munson 2000).

Generally, large diameter trees tend to be more attractive to infestation by bark beetles, indicating the usefulness of selecting trap trees that are most likely to become infested (Mezei et al. 2014) and effectively timing treatments for greatest impact. Use of felled or standing trap trees is a common sanitation tactic, but their effective use is dependent upon the environment (e.g. Fettig and Hilszczanski 2015). For example, during warm, dry winters with low snowpack, Holusa et al. (2017) recommend land managers fell trap trees just before bark beetle emergence in the spring to maximize efficacy, but during cooler, wetter winters with more snowpack, trap trees can be felled earlier in the winter, as these conditions maintain characteristics of the trap trees attractive to emerging beetles. Coupling push–pull strategies with silvicultural strategies designed to maintain vigorous trees and favoring less susceptible host trees for retention can aid in reducing pest population growth.

20.2.8   Silviculture and Biological Control

Biological control involves utilizing natural enemies (parasites, parasitoids, pathogens etc.) to achieve a reduction or control of pest populations. Increasing the size of established natural enemy populations (parasitoids, predators etc.) by releasing large numbers of individuals as defense against pests is referred to as augmentative biological control (Hoy 2004a). In contrast, classical biological control

(Hoy 2004b) involves introducing non-native natural enemies to establish populations to reduce non-native, invasive pest populations. A third option, conservation biological control, involves altering the vertical or horizontal structure, including species composition, of a given land unit to provide more habitat for natural enemies and thus maintain a reserve of beneficial insects within your forested stand.

Silviculture can actively promote conservation biological control, by manipulating the overstory composition or structure to increase understory growth or shift species composition to increase habitat reservoirs of beneficial natural enemy species, illustrating the direct link between silvicultural strategies and biological control in pest management. Classical and augmentative biological control can be used in concert with silvicultural treatments designed to promote individual tree vigor or increase or maintain horizontal and vertical stand structural complexity, including the use of species mixtures. For example, Perez-Alvarez et al. (2019) found classical and augmentative biological control to be more effective in complex than in simple landscapes. This highlights the potential for creation of complex forest structures, and landscape heterogeneity, to potentially increase the impact of biological control programs.

Traditional silviculture practice to meet timber production objectives has primarily utilized monocultures and even-aged regeneration methods (clearcut, seed tree and shelterwood methods) and thus result in reduced stand complexity. Even-aged monocultures can be more susceptible to insect outbreaks and large-scale damage and mortality. Increasing stand structural and compositional complexity increases natural enemy populations and relatively low pest populations (Klapwijk et al. 2016) while also enhancing resilience. For example, single-tree selection in uneven-aged stands increases shading of cut stumps, lowering the temperature of the stump surface and increasing development times for the large pine weevil larvae (*Hylobius abietis*), making them more vulnerable to predation (Inward et al. 2012). Predator population increases help to prevent the buildup of pest populations and thus can aid in preventing epidemic outbreaks (Klapwijk et al. 2016).

Warzée et al. (2006) calculated predator/prey ratios for the native European spruce bark beetle, *Ips typographus,* which primarily attacks spruce species, and the predator, the ant beetle (*Thanasimus formicarius*), in stands of different species compositions. They found that these ratios were significantly greater in mixed species stands, especially those stands with a substantial pine component, as the ant beetle finds more favorable pupation sites on thick barked pines compared to thinner barked spruce (Warzée et al. 2006). In this study, pine species were present on two sites, one composed of 26% pine, the other 80% pine, suggesting that pine as either a minor or major component can positively influence predator/prey ratios for this species (Warzée et al. 2006). Similarly, promotion of certain flowering species in agricultural settings can increase longevity of parasitoids, showing promise for similar use in forested stands (Russell 2015). Mixed species management can influence the life cycle and population levels of natural enemies thus additionally impacting pest species populations (Klapwijk et al. 2016). Incorporating native biodiversity into the silvicultural prescription allows for multiple objectives to be met in a single treatment.

When considering biological control of invasive species, natural enemies from their native habitat are often used as biological control agents in their introduced ranges (e.g. Cheah 2011; Bauer et al. 2015; Kenis et al. 2017). The abundance of invasive species is often greater in their invaded ranges, potentially due to their release from predation, and as such, invasive species often do not have natural enemies in their new habitats (the Enemy Release Hypothesis; Williamson 1996). This generally means that within their native ranges, populations are controlled by natural enemies and tree host defenses, however, when freed from natural predation and host defenses, they become much more damaging as populations rise. Many recent insect invasions around the world exhibit population growth supportive of this hypothesis, including the recent invasion of the emerald ash borer (*Agrilus planipennis*) in the eastern United States. This invasive beetle kills overstory ash species (*Fraxinus* spp.), significantly altering forest succession, and causing economic losses. Researchers and managers, as part of a classical biological control program, released a parasitoid, *Tetrastichus planipennisi,* of the emerald ash borer, which effectively reduced sapling mortality in emerald ash borer-infested stands in Michigan (Duan et al. 2017). While most ash species show little to no resilience to emerald ash borer, green ash (*Fraxinus pennsylvanica*) regenerates quickly after disturbance and reaches reproductive maturity relatively quickly (Kashian 2016). There is potential to sustain green ash by combining classical biological control with silviculture, creating stand conditions conducive to maintaining or increasing populations of the biological control agent and regeneration of green ash.

The sirex woodwasp has been an established non-native invasive pest for decades, recently arriving in the northeastern United States. Current silvicultural strategies involve thinning stands and removing smaller and suppressed size classes (Dodds et al. 2014). Establishment of the parasitic nematode, *Deladenus siricidicola,* for biological control has been successfully utilized in Australia (and elsewhere in the southern hemisphere) and shows promise, albeit with serious reservations, for expansion to North America (Haugen 1990; Bedding and Iede 2005; Bittner et al. 2019). Pines are introduced to Australia, meaning the risk to non-target organisms is minimal as insects in Australia did not co-evolve with pines and are rarely associated with the trees. In North America, there are communities of native insects associated with pines and, consequently, there are potential negative impacts for non-target organisms that warrant pause in applying this strategy. In a recent study, Bittner et al. (2019) evaluated strains of these nematodes within North America, and observed that native nematodes may both positively and negatively influence the sterilization success of sirex woodwasp. Other invasive insects, such as the balsam and hemlock woolly adelgids, have both been successfully preyed upon by a single species of beetle, *Sasajiscymnus tsugae,* in a laboratory setting, showing potential for this agent to be released as a classic biological control agent and further advance IPM strategies for both invasive species (Jetton et al. 2011).

Elkinton et al. (1996) found evidence that increased white-footed mouse (*Peromyscus leucopus*) density resulted in reduced spongy moth population density. Further, they also found a strong positive association between acorn density and

the white-footed mouse population, indicating the importance of acorns for over-wintering populations of white-footed mice. Strategies aimed at maximizing acorn production (e.g. low thinning, crop-tree release), as well as species composition manipulation, especially in low-risk stands, may help to maintain conditions less conducive to high spongy moth populations. This example illustrates how silviculture can promote conditions conducive to native predators (conservation biocontrol) for the control of non-native invasive insects, thereby aiding in reduction of pest populations and maintaining forest health.

20.2.9   Silviculture and Genetic Selection

Genetic selection, or selecting host trees that show promise of resistance to insect attack, and the establishment of breeding programs to propagate these "plus" trees, is a widely researched topic (Kinloch and Stonecypher 1969; McKeand et al. 2003; Roberds et al. 2003). Outside of traditional tree breeding programs, selection of trees in natural settings requires managers to select trees based on their phenotype; the underlying genotype is usually unknown. Exploiting these pre-adapted traits through the utilization of existing genetic variation in breeding programs is an effective method of characterizing resistance mechanisms within species, and then propagating progeny that show increased defensive capabilities. For example, Zas et al. (2017) characterized existing genetic variation in Norway spruce (*Picea abies*) traits related to increased resistance to the large pine weevil.

Land mangers currently use silvicultural strategies to minimize damage from this pest on artificial regeneration, including soil preparation and shelterwood treatments (Nordlander et al. 2011), however these may be difficult to apply or expensive. Therefore, the decision-making process land managers use to select treatment options is important. Consider Fig. 20.5, which highlights a general decision model including both silvicultural strategies and genetic selection can be utilized to manage plantations, as well as the research requirements for IPM (Alfaro et al. 1995). This demonstrates how genetic selection of putatively resistant and susceptible individuals, and subsequent silvicultural interventions along with other IPM strategies (biological control, etc.) create a framework to help guide land managers in establishing productive plantations that demonstrate the core principles of IPM. By including both resistant and susceptible individuals, one can assess how alternative management strategies (pruning, spacing, biological control) can reduce infestation levels.

Genetic host tree resistance can be categorized as constitutive or inducible. Constitutive defenses are those defenses that are always expressed, whereas induced defenses are those defenses a plant expresses in response to herbivory (Larsson 2002). Antibiosis indicates that some aspect of the host plant (chemical composition of tissues, defenses) has a negative impact on the pest biology (i.e. survival, development) (Painter 1958). For example, Bucholz et al. (2017) found that without direct contact, volatile organic compounds associated with the resistant Veitch fir (*Abies veitchii*) compared to a susceptible species, Fraser fir, resulted in significantly
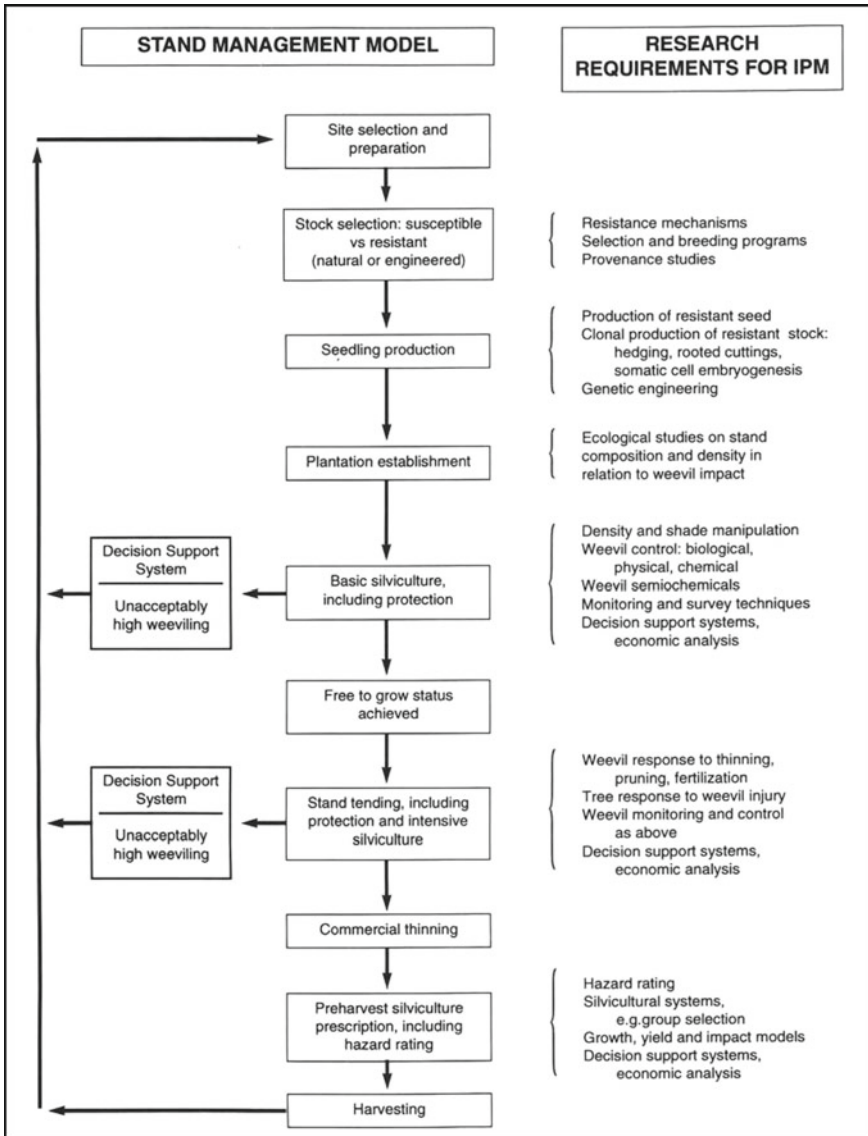
Fig. 20.5 Decision key for integrated pest management of Sitka spruce plantations to mitigate damage from the white pine weevil. Modified from Alfaro et al. (1995)

reduced eclosion success of balsam woolly adelgid eggs. This suggests an antibiotic effect of the constitutive chemicals released by Veitch fir on balsam woolly adelgid eggs.

Antixenosis or non-preference (e.g. Painter 1958), occurs when some aspect of the host, either chemical or morphological, results in reduced interaction (e.g.

feeding, oviposition) of the herbivore with the host. An example of this can be seen with the codling moth (*Cydia pomonella*) and leaf tissue metabolites from resistant and susceptible cultivars of apple trees (*Malus* spp). Significantly more oviposition occurred on cloth containing metabolites from susceptible than resistant cultivars, indicating oviposition preference based on chemical cues (Lombarkia and Derridj 2008).

Tolerance describes hosts that can sustain insect feeding activity without serious loss in productivity and is therefore subtly different from resistance (Painter 1958). Strauss and Agrawal (1999) defined tolerance as the degree to which plant fitness is impacted by herbivore damage relative to an undamaged state, whereas resistance was defined as any plant trait which reduced herbivore preference or performance. Tolerance mechanisms are therefore related to increased net photosynthetic rate after damage or compensatory action, high relative growth rates, root carbon storage for above-ground reproduction, and increased branching and resource allocations after damage (Strauss and Agrawal 1999 and references therein). An example of tolerance involves tannin concentration in quaking aspen leaves that does not serve as a defensive compound (i.e. resistance) but one that facilitates nutrient uptake post-defoliation (Madritch and Lindroth 2015). This is viewed as a tolerance mechanism, as the production of greater amounts of these types of secondary metabolites influences nutrient recoveries that may be hindered by defoliation damage.

Other resistance mechanisms, such as oleoresin production, are quantitative genetic traits that can be selected for during tree breeding programs. These traits are complex in that they are composed of many different "small effect" loci that contribute to tree phenotype (e.g. Mundt 2014). Ultimately, the goal is to breed host varieties resistant to certain pest species. Oleoresin flow, along with number of canals or preformed defensive (resin) ducts, has been shown to be positively correlated with survival following bark beetle attack. Bark beetle feeding activity slices through these canals or ducts, releasing their resin, which may envelop or remove the beetles; the more resin ducts a tree has, the more likely it is to successfully eject the attacking beetles (Strom et al. 2002; Kane and Kolb 2010).

In addition, seasonality, and its impact on physiological processes is an important consideration. Lorio (1986) used the framework of Loomis' (1932) growth-differentiation balance hypothesis to examine conditions ideal for southern pine beetle population expansion. He concluded that this hypothesis was useful in explaining seasonal demand for photosynthate, ultimately driving seasonal vulnerability to southern pine beetle. The trade-off between spring growth and defense suggests that fast-growing trees can be susceptible during these periods when growth processes use more available photosynthate, leaving less allocated towards defense production. The variance in this trait among populations of loblolly pine (*Pinus taeda*) is heritable.

Westbrook et al. (2013) developed a genomic prediction model across the range of loblolly pine, identifying specific genetic regions associated with increased oleoresin production. This work yielded a guide for making genetic selections to provide increased resistance to southern pine beetle. Trees with increased resistance can be incorporated into silviculture when regenerating stands. Planting all or part of the

stand with more resistant trees in anticipation of future insect herbivory, coupled with ongoing silvicultural strategies that promote tree vigor (thinning, adequate spacing etc.) would be an approach to increase resilience (Table 20.1) and may be an important step forward for bark beetle IPM.

Resistance within stands can be promoted by maintenance of stand density index [SDI; a measure of relative density using the relationship between average tree size and stand density (Reineke 1933)] below certain thresholds. For example, Long and Shaw (2005) review strategies associated with size/density relationships surrounding mountain pine beetle, and found that maintaining a SDI below 250 minimizes susceptibility to mountain pine beetle attack. The difficult aspect of management is prioritizing stands for treatment and connecting treatments across landscapes to decrease susceptibility. Reforestation, including planting with genetically improved genotypes where available and economically feasible, aids in contributing to decreased landscape-level susceptibility.

Earlier in the chapter, we discussed using silviculture to shift vertical and horizontal stand structure, with one outcome being increased vigor of residual trees. Individual tree response to reduced competition and increased resource availability is related to the genetic profile of the tree and the surrounding abiotic site conditions (the environment). Growth response to treatment can be optimized through appropriate silviculture in combination with genetic selection by retaining high vigor trees (those that allocate more stem wood per square meter leaf area), with the assumption that this trait is partially determined by genetics. Selecting trees with high growth rates prior to treatment can be challenging (Fischer et al. 2010) but may be possible through additional measurements of tree cores and crown area. Remote sensing applications can detect thinned stands with increased growth rates and therefore resistance to bark beetle attack, establishing a relatively easy method of monitoring overall stand resistance at large scales and across multiple land ownerships (Coops et al. 2009). Silviculturists need to consider the evolutionary adaptation occurring in the stand between bark beetles, host trees, and climate; for example bark beetles may be able to select for host trees least adapted to the changing climate (e.g. Six et al. 2018), resulting in a more resilient stand following bark beetle mortality.

Abiotic site conditions also play a key role in determining phenotypes. Abiotic site conditions (e.g. slope, aspect, topography, soil conditions) tend to change slowly through time or not at all. The abiotic capacity of a site to produce vegetation is often used as a proxy for site quality; high (good) sites produce more vegetation than low (poor) sites. Vegetation production is less on low sites due to limiting resources for plant growth, often related to poor soil resources. The relationship between site conditions and resistance to insects is highly dependent upon the tree host species and corresponding pest species. Slow-growing individuals may be more susceptible to attack by certain insects (i.e. subalpine fir (*Abies lasiocarpa*) by the western balsam bark beetle (*Dryocoetes confusus*), therefore considerations of site quality and genetics of growing stock (whether natural or artificial) are important for decreasing susceptibility to insect attack (Bleiker et al. 2005). For example, slower-growing Eucalypts (*Eucalyptus* spp.) are recommended for low quality sites, since slower growing tree foliage may be better defended against defoliation (Stone

2001). Managers face a complexity of decisions related to the interactions between silviculture, genetic selection, and underlying site factors. After carefully considering these interactions, silviculture and genetic selection can be important components of successful IPM programs.

20.3   Silviculture Over Long Temporal and Large Spatial Scales

The impacts of silviculture extend over long temporal and large spatial scales. Understanding the role of individual stands at these large scales is an important consideration when selecting the appropriate silvicultural strategy because individual stands are connected to form a landscape. Silvicultural treatments necessitate understanding and predicting patterns of tree and stand growth at large spatial and long temporal scales, including interactions with various disturbances and incorporating uncertainty into predictive models. However, understanding these predictions and then designing appropriate strategies that meet multiple goals and objectives is a necessary component of building resistant and resilient landscapes.

Building resistance to insect pests at smaller spatial scales highlights the difficulties faced by silviculturists by both long time scales and scaling up to a landscape. For example, stands at risk to spruce bark beetle have common structural characteristics that can be manipulated through management thereby reducing risk. At the stand-scale, this would entail reducing the relative proportion of overstory basal area in host spruce, reducing the average size of spruce in the stand, or reducing stand basal area (Schmid and Frye 1976). However, while an individual stand may be treated, building this resistance at landscape-scales in practice has proved unrealistic due to economic and political constraints (DeRose and Long 2014). Having adjacent stands that are left untreated provides environments capable of allowing pest insect populations to grow. Once populations have reached epidemic levels, resistant stands become susceptible. Strategically placed area treatments (SPLATs, Finney 2001) are useful in reducing fire severity while only treating ~ 20% of the landscape, however, the efficacy of this practice for insect outbreak remains untested. Resistance is a temporally defined window that changes continually as stands grow and develop after treatment. In the case of spruce bark beetle, the maintenance of resistance at a stand-scale would require multiple treatments to maintain vigor of residual spruce, eventually resulting in structures susceptible to spruce beetle outbreak (Schmid and Frye 1976; DeRose and Long 2014). Therefore, focusing solely on building resistance to a pest may be unproductive. Instead, land managers should focus on a dual approach of targeted treatments in high-risk stands, as well as building resilience through maintaining diversity in both age class structure and species composition across the landscape. In many instances where public and private lands are interspersed, training and shared stewardship programs can help bring private landowners and other stakeholders into

the decision-making process alongside silviculturists and other land managers (e.g. Neely et al. 2011).

Building resilience across larger temporal and spatial scales adds complexity to assessing silvicultural strategies at smaller scales. For example, quaking aspen across the western and southwestern United States has experienced large-scale droughts over the past decade. As a result, Sudden Aspen Decline, which is a complex progression of physiological stress, insect infestation and disease, has degraded and caused wide-spread mortality in many stands (Worrall et al. 2010). This decline is complex because it involves multiple agents of mortality, starting with abiotic stress (drought) creating conditions conducive to attack by mostly secondary pests. Increased numbers of susceptible, stressed host trees have allowed an increase in secondary mortality-causing pest populations, and therefore their increased ability to be a major driver of mortality within these stands. Insects such as bronze poplar borer (*Agrilus liragus*) and aspen bark beetles (e.g. *Trypophloeus populi*) are viewed as contributing agents in this decline complex, where abiotic factors are considered inciting events (Worrall et al. 2010). Therefore, assessing site characteristics that predispose stands to drought may help managers prioritize stands for silvicultural strategies designed to increase the ability to recover following abiotic disturbance. Landscape-scale resilience can be increased by reducing the proportion of drought-susceptible stands in the landscape. Examples of strategies to increase drought resistance and resilience include thinning to increase individual tree vigor, clearfelling the overstory to regenerate the stand, or shifting species composition toward more drought tolerant species.

The rate at which climate change is occurring highlights the challenge in adapting management. Understanding how abiotic conditions can both cause mortality and stress, therefore creating conditions conducive for attack by biotic agents, is an important concept in promoting resilience at a landscape scale. Although trees have the ability to cope with climate stressors (e.g. stomatal regulation, migration to new areas), rapid climatic change and the concomitant alteration of insect pest populations creates uncertainty in tree host species acclimation potential (Rehfeldt 2006). Evolutionary adaptation and migration work on much slower scales in perennial woody species than in annual species. Generation times are slower in forested ecosystems, and therefore large-scale abiotic changes, along with accompanying biotic changes (e.g. native/invasive species ranges, increased reproductive generations) may inhibit their natural abilities to adapt to altered conditions. Concepts like assisted migration (Sensu Aitken et al. 2008) and assisted gene flow (Sensu Aitken and Whitlock 2013) exist to represent this human-aided transition of species to new areas currently outside their range, but require adequate forethought and forecasting to help determine where to move species and how to genetically bolster species in situ.

20.3.1 Adaptive Silviculture for Climate Change

Studies aimed at developing ecologically-based silvicultural treatments for the future in different ecosystems are needed to understand the complex interactions between

Fig. 20.6 Silvicultural strategies being investigated in the adaptive silviculture for climate change program. From Nagel et al. (2017)
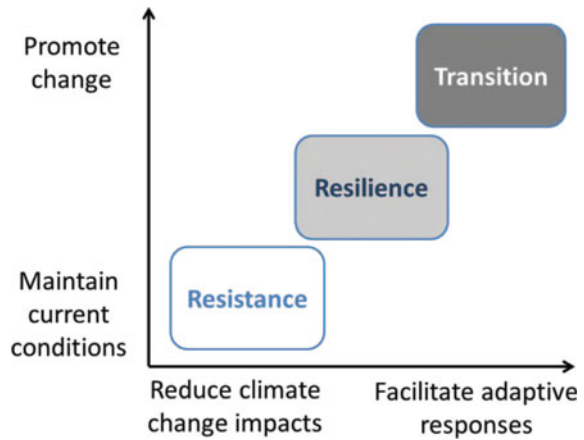
ecological components under rapid climatic change. An ongoing effort in the United States, referred to as the Adaptive Silviculture for Climate Change (ASCC) program, is one such study (Nagel et al. 2017). As a result of the continuing impact of climate change and the primarily unknown effects of interactions between climate change and both native and non-native insect pests (Weed et al. 2013), there is a need to develop silvicultural strategies now that can benefit forests in the future. The overarching goal of the ASCC is to understand different silvicultural strategies focused around three central approaches: Resistance, Resilience and Transition (Nagel et al. 2017). Figure 20.6 details how each of the above categories fits into management, and the level of change associated with each (Nagel et al. 2017).

Given the uncertainty of climate change predictions, as well as the heterogeneous impact of various abiotic and biotic stressors at different locations, ASCC attempts to address how different silvicultural strategies can be used to meet land management goals at varying time scales and across regions and ecotypes. The three approaches represent an increasing scale of change. The resistance approach maintains the "status quo", the resilience approach maintains overstory tree vigor while opening growing space for natural regeneration and the transition approach focuses on shifting composition toward trees considered better suited for an uncertain climatic future. The resistance approach increases the ability of current stands to withstand change, while the resilience and transition approaches attempt to accommodate a moderate-to-large amount of change and a shift away from the current structure and/or species composition. This large-scale research project will yield valuable information for silviculturists attempting to sustain healthy stands and forests under an increasingly uncertain and complex future.

20.4   Synthesis and Conclusion

Use of silviculture to manipulate either vertical and horizontal structure or species composition will also impact the trajectory of stand development and the timing of changes within the stand (stand dynamics) (Oliver and Larson 1996). Silviculture results in a disturbance, and depending upon the number and pattern of trees removed, can effectively shift stands in different directions along a stand development continuum. For example, a dense, even-aged stand under high competition that has the overstory density reduced to below full site occupancy will shift from stem exclusion into understory re-initiation as a new age class develops in the understory. While this transition would occur naturally without silvicultural intervention, with silviculture, a stand can shift overnight from one stage to another, greatly increasing the rate of change and altering the process of stand development.

Silviculturists must be able to predict changes to stand development patterns following treatment. This is most frequently achieved using models (e.g. the Forest Vegetation Simulator; Dixon 2002) and before-after monitoring data. Analysis of before-after data allows the silviculturist to adapt the treatment plan as necessary through time. Silviculturists must also understand and watch for the interactions between silviculture, forest insects and diseases, and other disturbances and provide for appropriate mitigation strategies where necessary.

The approach of managing forest insects through increased resistance and/or resilience can be effectively met using silvicultural strategies. These include strategies developed in conjunction with other management tools in an IPM program. Specific silvicultural prescriptions will vary depending upon stand conditions, site factors, and host tree and pest ecology. However, research and experience indicate that similar results can be expected under specific stand vertical and horizontal structures (Table 20.1) and species composition. From simple to quite complex, using silviculture to manage forest insects can be challenging. Only those (e.g. forest health specialists, forest managers) with advanced training should attempt to resolve forest insect problems in multiaged, mixed species stands without aid from a more experienced silviculturist. Silviculture continues to be an important addition to most forest insect management strategies, and approaching it from a resistance and resilience framework is likely to be successful under rapidly changing environmental and social conditions.

References

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol Appl 95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Aitken SN, Whitlock MC (2013) Assisted gene flow to facilitate local adaptation to climate change. Annu Rev Ecol Evol Syst 44:367–388. https://doi.org/10.1146/annurev-ecolsys-110512-135747

Alfaro RI, Borden JH, Fraser RG, Yanchuck AD (1995) The white pine weevil in British Columbia: basis for an integrated pest management system. For Chron 7(1):66–73

Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, … Zeppel M (2015) Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol 208(3):674–683. https://doi.org/10.1111/nph.13477

Anhold JA, Jenkins MJ, Long JN (1996) Technical commentary: management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. West J Appl for 11(2):50–53. https://doi.org/10.1093/wjaf/11.2.50

Asaro C, Nowak JT, Elledge A (2017) Why have southern pine beetle outbreaks declined in the Southeastern U.S. with the expansion of intensive pine silviculture? a brief review of hypotheses. For Ecol Manage 391:338–348. https://doi.org/10.1016/J.FORECO.2017.01.035

Bauer LS, Duan JJ, Gould JR, Driesche RV (2015) Progress in the classical biological control of *Agrilus planipennis* Fairmaire (Coleoptera:Buprestidae) in North America. Can Entomol 317:300–317. https://doi.org/10.4039/tce.2015.18

Bedding RA, Iede ET (2005) Ch. 21: Application of *Beddingia siricidicola* for sirex woodwasp control. In: Grewal PS, Ehlers RU, Shapiro-Ilan DI (eds) Nematodes as biocontrol agents. CAB International.

Bentz B, Logan J, MacMahon J, Allen CD, Ayres M, Berg E, … Wood D (2009) Bark beetle outbreaks in western North America: causes and consequences. Bark Beetle Symposium; Snowbird, Utah; November, 2005. University of Utah Press, Salt Lake City, UT, p 42.

Bentz BJ, Munson AS (2000) Spruce beetle population suppression in Northern Utah. West J Appl For 15(3):122–128. https://doi.org/10.1093/wjaf/15.3.122

Billings RF, Clarke SR, Mendoza VE, Cabrera PC, Figueroa BM, Campos JR, Baeza G (2004) Bark beetle outbreaks and fire: a devastating combination for Central America's pine forests. Forest Chem Rev 124(6):10–15

Bittner TD, Havill N, Caetano IAL, Hajek AE (2019) Efficacy of Kamona strain *Deladenus siricidicola* nematodes for biological control of *Sirex noctilio* in North America and hybridisation with invasive conspecifics. NeoBiota 44:39–55

Bleiker KP, Lindgren BS, Maclauchlan LE (2005) Resistance of fast- and slow-growing subalpine fir to pheromone- induced attack by Western balsam bark beetle (Coleoptera: Scolytinae). Agric For Entomol 7:237–244

Borden JH, Birmingham AL, Burleigh JS (2006) Evaluation of the push-pull tactic against the mountain pine beetle using verbenone and non-host volatiles in combination with pheromone-baited trees. For Chron 82(4):579–590

Brantley ST, Mayfield AE, Jetton RM, Miniat CF, Zietlow DR, Brown CL, Rhea JR (2017) Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested Eastern hemlock seedlings. For Ecol Manage 385:150–160. https://doi.org/10.1016/j.foreco.2016.11.028

Brookes M, Colbert J, Mitchell R, Stark R (eds) (1985) Managing trees and stands susceptible to western spruce budworm. USDA Forest Service Cooperative State Research Service Technical Bulletin No. 1695, Washington, DC

Brookes M, Campbell RW, Colbert JJ, Mitchell RG, Stark RW (eds) (1987) Western spruce budworm. USDA Forest Service Cooperative State Research Service Technical Bulletin No. 1694, Washington, DC

Brookes M, Stark R, Campbell R (eds) (1978) The Douglas-fir tussock moth: a synthesis. USDA Forest Service Science and Education Agency Technical Bulletin 1585, Washington, DC

Bucholz E, Frampton J, Jetton RM, Tilotta D, Lucia L (2017) Effect of different headspace concentrations of bornyl acetate on fecundity of green peach aphid and balsam woolly adelgid. Scand J For Res. https://doi.org/10.1080/02827581.2016.1275769

Carlson CE, Fellin DG, Schmidt WC (1983) The Western spruce budworm in Northern Rocky mountain forests: a review of ecology, insecticidal treatments and silvicultural practices. In: OLaughlin J, Pfister RD (eds) Management of second growth forests, the state of knowledge

and research needs. Montana Forest Conservation Experiment Station, University of Montana, Missoula, Missoula, MT, pp 76–103

Cheah C (2011) *Sasjiscymnus* (= *Pseudoscymnus*) *tsugae*, a ladybeetle from Japan. In: Onken B, Reardon R (eds) Implementation and status of biological control of the hemlock woolly adelgid. FHTET-2011–04. U.S. Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team: 43–52. Chapter 4, Morgantown, WV

Cook SM, Khan ZR, Pickett JA (2007) The use of push-pull strategies in integrated pest management. Ann Rev Entomol 52:375–400. https://doi.org/10.1146/annurev.ento.52.110405.091407

Coops NC, Waring RH, Wulder MA, White JC (2009) Remote sensing of environment prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. Remote Sens Environ 113(5):1058–1066. https://doi.org/10.1016/j.rse.2009.01.013

D'Amato AW, Bradford JB, Fraver S, Palik BJ (2013) Effects of thinning on drought vulnerability and climate response in North temperate forest ecosystems. Ecol Appl 23(8):1735–1742

De Groot P, Hopkin AA, Sajan RJ (2005) Silvicultural techniques and guidelines for the management of major insects and diseases of spruce, pine and aspen in Eastern Canada. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, Ont, p 65

DeRose RJ, Long JN (2007) Disturbance, structure, and composition: spruce beetle and engelmann spruce forests on the Markagunt Plateau, Utah. For Ecol Manag 244(1–3):16–23. https://doi.org/10.1016/j.foreco.2007.03.065

DeRose RJ, Long JN (2014) Resistance and resilience: a conceptual framework for silviculture. Forest Sci 60(6):1205–1212. https://doi.org/10.5849/forsci.13-507

Dixon GE, C. (2002). Essential FVS: A user's guide to the forest vegetation simulator. U.S. Department of Agriculture Forest Service, Forest Management Center, Internal Rep. Fort Collins, CO

Dodds KJ, Cooke RR, Gilmore DW (2007) Silvicultural options to reduce pine susceptibility to attack by a newly detected invasive species, *Sirex noctilio*. North J Appl For 24(3):165–167

Dodds K, Cooke R, Hanavan R (2014) The effects of silvicultural treatment on sirex noctilio attacks and tree health in Northeastern United States. Forests 5(11):2810–2824. https://doi.org/10.3390/f5112810

Duan JJ, Bauer LS, Van Driesche RG (2017) Emerald ash borer biocontrol in ash saplings: The potential for early stage recovery of North American ash trees. For Ecol Manage 394:64–72. https://doi.org/10.1016/j.foreco.2017.03.024

Elek J, Wardlaw T (2013) Options for managing Chrysomelid leaf beetles in Australian eucalypt plantations: reducing the chemical footprint. Agric For Entomol 15:351–365. https://doi.org/10.1111/afe.12021

Elkinton JS, Healy WM, Buonaccorsi JP, Boettner GH, Hazzard AM, Smith HR (1996) Interactions among gypsy moths, white-footed mice, and acorns. Ecology 77(8):2332–2342

Fajvan MA, Gottschalk KW (2012) The effects of silvicultural thinning and *Lymantria dispar* L. defoliation on wood volume growth of *Quercus* spp. American J Plant Sci 03(02):276–282. https://doi.org/10.4236/ajps.2012.32033

Fettig C, Gibson K, Munson A, Negrón J (2014) A comment on "management for mountain pine beetle outbreak suppression: does relevant science support current policy?" Forests 5(4):822–826. https://doi.org/10.3390/f5040822

Fettig CJ, Hilszczanski J (2015) Management strategies for bark beetles in conifer forests. In: Vega F, Hofstetter R (eds) Bark beetles: biology and ecology of native and invasive species. Academic Press

Fettig CJ, Klepzig KD, Billings RF, Munson AS, Nebeker TE, Negrón JF, Nowak JT (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the Western and Southern United States. For Ecol Manag 238(1–3):24–53. https://doi.org/10.1016/J.FORECO.2006.10.011

Fettig CJ, McKelvey SR, Borys RR, Dabney P, Hamud SM, Nelson LJ, Seybold SJ (2009) Efficacy of verbenone for protecting ponderosa pine stands from western pine beetle (Coleoptera: Curculionidae: Scolytinae) attack in California. J Econ Entomol 102(5):1

Fettig CJ, Munson AS (2020) Efficacy of verbenone and a blend of verbenone and nonhost volatiles for protecting lodgepole pine from mountain pine beetle (Coleoptera: Curculionidae). Agric For Entomol. https://doi.org/10.1111/afe.12392

Finney MA (2001) Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. Forest Sci 47(2):219–228. https://doi.org/10.1093/forestscience/47.2.219

Fischer MJ, Waring KM, Hofstetter RW, Kolb TE (2010) Ponderosa pine characteristics associated with attack by the roundheaded pine beetle. Forest Sci 56(5):473–483

Fuentealba A, Bauce E (2011) Site factors and management influence short-term host resistance to spruce budworm, *Choristoneura fumiferana* (Clem.), in a species-specific manner. Pest Manag Sci, 245–253. https://doi.org/10.1002/ps.2253

Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yepez EA, Macalady AK, Pangle RE, McDowell NG (2013) Drought predisposes piñon–juniper woodlands to insect attacks and mortality. New Phytol 198:567–578. https://doi.org/10.1111/nph.12174

Gillette NE, Kegley SJ, Costello SL, Mori SR, Webster JN, Mehmel CJ, Wood DL (2014) Efficacy of verbenone and green leaf volatiles for protecting whitebark and limber pines from attack by mountain pine beetle (Coleoptera: Curculionidae: Scolytinae). Environ Entomol 43(4):1019–1026. https://doi.org/10.1603/EN12330

Gillette NE, Mehmel CJ, Mori SR, Webster JN, Wood DL, Erbilgin N, Owen DR (2012) The push—pull tactic for mitigation of mountain pine beetle (Coleoptera: Curculionidae) damage in lodgepole and whitebark pines. Environ Entomol 41(6):1575–1586

Gilmore DW, Palik BJ (2006) A revised managers handbook for red pine in the North Central Region. U.S. Department of Agriculture, Forest Service, North Central Research Station, Saint Paul, MN. General Technical Report NC-264, 1–55

Gottschalk KW (1993) Silvicultural guidelines for forest stands threatened by the gypsy moth. US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. General Technical Report NE-171

Hadfield JS, Flanagan PT (2000) Dwarf mistletoe pruning may induce Douglas-fir beetle attacks. West J Appl for 15(1):34–36. https://doi.org/10.1093/wjaf/15.1.34

Hansen EM, Negron JF, Munson AS, Anhold JA (2010) A retrospective assessment of partial cutting to reduce spruce beetle-caused mortality in the Southern Rocky Mountains. West J Appl for 25(2):81–87

Haugen D (1990) Control procedures for *Sirex noctilio* in the green triangle: review from detection to severe outbreak. Aust For 53:24–32

Helms J (ed) (1998) The dictionary of forestry. The Society of American Foresters, Bethesda, MD

Hoebeke ER, Haugen DA, Haack RA (2005) *Sirex noctilio*: discovery of a Palearctic wood wasp in New York. Newsletter Michigan Entomol Soc 50(1 and 2):24–25

Holusa J, Hlasny T, Modlinger R, Lukásova K, Kula E (2017) Felled trap trees as the traditional method for bark beetle control: can the trapping performance be increased? For Ecol Manage 404:165–173. https://doi.org/10.1016/j.foreco.2017.08.019

Hoy M.A. (2004a). Augmentative biological control. In: Encyclopedia of entomology. Springer, Dordrecht

Hoy M.A. (2004b). Classical biological control. In: Encyclopedia of entomology. Springer, Dordrecht

Inward DJG, Wainhouse D, Peace A (2012) The effect of temperature on the development and life cycle regulation of the pine weevil *Hylobius abietis* and the potential impacts of climate change. Agric For Entomol 348–357. https://doi.org/10.1111/j.1461-9563.2012.00575

Jetton RM, Monahan JF, Hain FP (2011) Laboratory studies of feeding and oviposition preference, developmental performance, and survival of the predatory beetle, *Sasajiscymnus tsugae* on diets of the woolly adelgids, *Adelges tsugae* and *Adelges piceae*. J Insect Sci 11(1):14. https://doi.org/10.1673/031.011.6801

Kane JM, Kolb TE (2010) Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. Oecologia 601–609. https://doi.org/10.1007/s00442-010-1683-4

Kane JM, Varner JM, Metz MR, van Mantgem PJ (2017) Characterizing interactions between fire and other disturbances and their impacts on tree mortality in Western U.S forests. For Ecol Manage 405:188–199. https://doi.org/10.1016/J.FORECO.2017.09.037

Kashian DM (2016) Sprouting and seed production may promote persistence of green ash in the presence of the emerald ash borer. Ecosphere 7:1–15

Kashian DM, Jackson RM, Lyons HD (2011) Forest structure altered by mountain pine beetle outbreaks affects subsequent attack in a Wyoming lodgepole pine forest, USA. Can J for Res 41(12):2403–2412. https://doi.org/10.1139/x11-142

Kegley SJ, Livingston RL, Gibson KE (1997) Pine engraver, Ips pini (Say), in the Western United States. U.S. Department of Agriculture Forest Service, Forest Insect and Disease Leaflet 122

Kenis M, Hurley BP, Hajek AE, Cock MJW (2017) Classical biological control of insect pests of trees: facts and figures. Biol Invas 19(11):3401–3417. https://doi.org/10.1007/s10530-017-1414-4

Kinloch BB, Stonecypher RW (1969) Genetic variation in susceptibility to fusiform rust in seedlings from a wild population of loblolly pine. Phytopathology 59:1246–1255

Klapwijk MJ, Bylund H, Schroeder M, Bjorkman C (2016) Forest management and natural biocontrol of insect pests. Forestry 89:253–262. https://doi.org/10.1093/forestry/cpw019

Klutsch JG, Shamoun SF, Erbilgin N (2017) Drought stress leads to systemic induced susceptibility to a nectrotrophic fungus associated with mountain pine beetle in *Pinus banksiana* seedlings. PLoS ONE 12(12):e0189203. https://doi.org/10.1371/journal.pone.0189203

Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, … Weed AS (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. For Ecol Manage 380:321–334. https://doi.org/10.1016/J.FORECO.2016.04.051

Kollenberg CL, O'Hara KL (1999) Leaf area and tree increment dynamics of even-aged and multiaged lodgepole pine stands in Montana. Can J For Res 29:687–695

Larsson S (2002) Chapter 1: Resistance in trees to insects—an overview of mechanisms and interactions. In: Wagner MR, Clancy KM, Lieutier F, Paine TD (eds) Mechanisms and deployment of resistance in trees to insects. Kluwer Academic Publishers, Norwell, MA, pp 1–31

Lombarkia N, Derridj S (2008) Resistance of apple trees to *Cydia pomonella* egg-laying due to leaf surface metabolites. Entomol Exp Appl 128:57–65. https://doi.org/10.1111/j.1570-7458.2008.00741.x

Long JN, Shaw JD (2005) A density management diagram for even-aged ponderosa pine stands. West J Appl For 20(4):205–215

Loomis WE (1932) Growth-differentiation balance vs carbohydrate-nitrogen ratio. Proc American Horticult Soc 29:240–245

Lorio PL (1986) Growth-differentiation balance: A basis for understanding Southern pine beetle-tree interactions. For Ecol Manage 14(4):259–273. https://doi.org/10.1016/0378-1127(86)90172-6

Madritch MD, Lindroth RL (2015) Condensed tannins increase nitrogen recovery by trees following insect defoliation. New Phytol 208:410–420

Massad TJ, Dyer LA (2010) A meta-analysis of the effects of global environmental change on plant-herbivore interactions. Arthropod-Plant Interac 4:181–188. https://doi.org/10.1007/s11829-010-9102-7

McDowell NG, Adams HD, Bailey JD, Kolb TE (2007) The role of stand density on growth efficiency, leaf area index, and resin flow in Southwestern ponderosa pine forests. Can J For Res 37(2):343–355. https://doi.org/10.1139/X06-233

McGregor MD, Amman GD, Schmitz RF, Oakes RD (1987) Partial cutting lodgepole pine stands to reduce losses to the mountain pine beetle. Can J for Res 17(10):1234–1239. https://doi.org/10.1139/x87-191

McHugh CW, Kolb TE, Wilson JL (2003) Bark beetle attacks on ponderosa pine following fire in Northern Arizona. Environ Entomol 32(3):510–522. https://doi.org/10.1603/0046-225X-32.3.510

McIntire T (1988) Forest health through silviculture and integrated pest management: a strategic plan. U.S. Department of Agriculture, Forest Service

McKeand SE, Amerson HV, Li B, Mullin TJ (2003) Families of loblolly pine that are the most stable for resistance to fusiform rust are the least predictable. Can J For Res 33:1335–1339

Mezei P, Grodzki W, Bazenec M, Škvarenina J, Brandysova V, Jakus R (2014) Host and site factors affecting tree mortality caused by the spruce bark beetle (*Ips typographus*) in mountainous conditions. For Ecol Manage 331:196–207. https://doi.org/10.1016/j.foreco.2014.07.031

Miller JM, Keen FP (1960) Biology and control of the western pine beetle. USDA Forest Service Misc. Pub. 800

Mitchell R, Waring RH, Pitman G (1983) Thinning lodgepole pine increases tree vigor and resistance to mountain pine beetle. For Sci 29(1):204–211

Morris JL, Cottrell S, Fettig CJ, Hansen WD, Sherriff L, Carter VA, … Sepp HT (2017) Managing bark beetle impacts on ecosystems and society: priority questions to motivate future research. J Appl Ecol 54:750–760. https://doi.org/10.1111/1365-2664.12782

Mundt CC (2014) Durable resistance: a key to sustainable management of pathogens and pests. Infect Genet Evol 27:446–455. https://doi.org/10.1016/j.meegid.2014.01.011

Muzika RM, Liebhold AM (2000) A critique of silvicultural approaches to managing defoliating insects in North America. Agric For Entomol 2:97–105. https://doi.org/10.1046/j.1461-9563.2000.00063.x

Nagel LM, Palik BJ, Battaglia MA, D'Amato AW, Guldin JM, Swanston CW, … Peterson DL (2017) Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. J Forest 115(3):167–178

Naidoo R, Lechowicz MJ (2001) Effects of gypsy moth on radial growth of deciduous trees. For Sci 47(3):338–348. https://doi.org/10.1093/forestscience/47.3.338

Neely B, Rondeau R, Sanderson J, Pague C, Kuhn B, Siemers J, Grunau L, Robertson J, McCarthy P, Barsugli J, Schulz T, Knapp C (2011) Gunnison basin: climate change vulnerability assessment for the Gunnison Climate Working Group, The Nature Conservancy, Colorado Natural Heritage Program, Western Water Assessment, University of Colorado, Boulder, and University of Alaska, Fairbanks. Project of the Southwest Climate Change Initiative, Boulder, CO, USA

Nordlander G, Hellqvist C, Johansson K, Nordenhem H (2011) Regeneration of European boreal forests: effectiveness of measures against seedling mortality caused by the pine weevil *Hylobius abietis*. For Ecol Manage 262:2354–2363

Nowak J, Asaro C, Klepzig K, Billings R (2008) The southern pine beetle prevention initiative: working for healthier forests. J Forest 106(5):261–267

Nowak JT, Meeker JR, Coyle DR, Steiner CA, Brownie C (2015) Southern pine beetle infestations in relation to forest stand conditions, previous thinning, and prescribed burning: evaluation of the Southern pine beetle prevention program. J Forest 113(5):454–462. https://doi.org/10.5849/jof.15-002

NPS Environmental Assessment (2007) Hemlock woolly adelgid control strategies along the Blue Ridge Parkway. US National Park Service: Blue Ridge Parkway

O'Hara KL (2014) Multiaged silviculture: managing for complex forest stand structure. Oxford University Press, Oxford, United Kingdom

Oliver CD, Larson BC (1996) Forest stand dynamics, Update. John Wiley and Sons Inc, New York

Ostry ME, Laflamme G, Katovich SA (2010) Silvicultural approaches for management of Eastern white pine to minimize impacts of damaging agents. For Pathol 40(3–4):332–346. https://doi.org/10.1111/j.1439-0329.2010.00661.x

Painter RH (1958) Resistance of plants to insects. Ann Rev Entomol 3:267–290

Perez-Alvarez R, Nault BA, Poveda K (2019) Effectiveness of augmentative biological control depends on landscape context. Sci Rep 9(1):1–15. https://doi.org/10.1038/s41598-019-45041-1

Pitt D, Hoepting M, Parker W, Morneault A, Lanteigne L, Stinson A, … Farrell JCG (2016) Optimum vegetation conditions for successful establishment of planted Eastern white pine (*Pinus strobus* L.). Forests 7(12):175. https://doi.org/10.3390/f7080175

Polinko A (2014) Stand response to western spruce budworm defoliation and mortality in New Mexico. Master of Science Thesis, School of Forestry, Northern Arizona University

Progar RA, Gillette N, Fettig CJ, Hrinkevich K (2014) Applied chemical ecology of the mountain pine beetle. For Sci 60(3):414–433. https://doi.org/10.5849/forsci.13-010

Rapp M (2017) Effects of western spruce budworm in mixed conifer forests of New Mexico. Master of Science Thesis, School of Forestry, Northern Arizona University

Rehfeldt GE (2006) A spline model of climate for the Western United States. USDA Forest Service General Technical Report RMRS-GTR-165, Rocky Mountain Research Station, Fort Collins, Colorado, USA

Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627–638

Reynolds KM, Holsten EH (1994) Relative importance of risk factors for spruce beetle outbreaks. Can J For Res 24(10):2089–2095. https://doi.org/10.1139/x94-268

Roberds JH, Strom BL, Hain FP, Gwaze DP, Mckeand SE, Lott LH (2003) Estimates of genetic parameters for oleoresin and growth traits in juvenile loblolly pine. Can J For Res 33:2469–2476. https://doi.org/10.1139/X03-186

Russell M (2015) A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species. Biol Control 82:96–103. https://doi.org/10.1016/j.biocontrol.2014.11.014

Ryan MG, Sapes G, Sala A, Hood SM (2015) Tree physiology and bark beetles. New Phytol 205:955–957. https://doi.org/10.1111/nph.13256

Savage M (1994) Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest in California. Can J For Res 24(6):1149–1159. https://doi.org/10.1139/x94-152

Schmid JM, Frye RH (1976) Stand ratings for spruce beetles. Research Note RM-309, US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station

Schmid JM, Frye RH (1977) Spruce beetle in the rockies. USDA Forest Service General Technical Report RM-49, Rocky Mountain Forest and Range Experiment Station

Schmid JM, Mata SA (2005) Mountain pine beetle-caused tree mortality in partially cut plots surrounded by unmanaged stands. Research Paper RMRS-RP-54. US Department of Agriculture, Forest Service, Rocky Mountain Research Station. https://doi.org/10.2737/RMRS-RP-54

Schoettle AW, Sniezko RA (2007) Proactive intervention to sustain high-elevation pine ecosystems threatened by white pine blister rust. J for Res 12:327–336. https://doi.org/10.1007/s10310-007-0024-x

Sidebottom J (2009) Balsam woolly adelgid: Christmas tree notes. North Carolina State University Extension Publications

Six DL, Vergobbi C, Cutter M (2018) Are survivors different? genetic-based selection of trees by mountain pine beetle during a climate change-driven outbreak in a high-elevation pine forest. Front Plant Sci 9:993

Sohn JA, Saha S, Bauhus J (2016) Potential of forest thinning to mitigate drought stress: a meta-analysis. For Ecol Manage 380:261–273. https://doi.org/10.1016/J.FORECO.2016.07.046

Stiell WM, Berry AB (1985) Limiting white pine weevil attacks by side shade. For Chron 61(1):5–9. https://doi.org/10.5558/tfc61005-1

Stone C (2001) Reducing the impact of insect herbivory in eucalypt plantations through management of extrinsic influences on tree vigour. Austral Ecol 482–488

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14(5):179–185. https://doi.org/10.1016/S0169-5347(98)01576-6

Strom BL, Goyer RA, Ingram LL Jr, Boyd GDL, Lott LH (2002) Oleoresin characteristics of progeny of loblolly pines that escaped attack by the Southern pine beetle. For Ecol Manage 158(1–3):169–178

Thomas Z, Waring KM (2015) Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in Northern New Mexico, USA. Forest Sci 61(1). https://doi.org/10.5849/forsci.13-085

Vane E, Waring KM, Polinko A (2017) The influence of Western spruce budworm on fire in spruce-fir forests. Fire Ecol 13(1):16–33. https://doi.org/10.4996/fireecology.1301016

Walker B, Holling CS, Carpenter SR, Kinzig A (2004) Resilience, adaptability and transformability in social–ecological systems. Ecol Soc 9(2):5. https://doi.org/10.2307/26267673

Waring RH, Pitman GB (1980) A simple model of host resistance to bark beetles. Oregon State University Forest Research Laboratory Research Note 65

Warzée N, Gilbert M, Grégoire J (2006) Predator/prey ratios: a measure of bark-beetle population status influenced by stand composition in different French stands after the 1999 storms. Ann For Sci 63:301–308. https://doi.org/10.1051/forest

Weed AS, Ayres MP, Hicke JA (2013) Consequences of climate change for biotic disturbances in North American forests. Ecol Monogr 83(4):441–470. https://doi.org/10.1890/13-0160.1

Westbrook JW, Resende MF Jr, Munoz P, Walker AR, Wegrzyn JL, Nelson CD, … Peter GF (2013) Association genetics of oleoresin flow in loblolly pine: discovering genes and predicting phenotype for improved resistance to bark beetles and bioenergy potential. New Phytol 199(1):89–100

Williamson M (1996) Biological invasions. Springer, Netherlands

Windmuller-Campione MA, Long JN (2015) If long-term resistance to a spruce beetle epidemic is futile, can silvicultural treatments increase resilience in spruce-fir forests in the Central Rocky Mountains? Forests 6:1157–1178. https://doi.org/10.3390/f6041157

Worrall JJ, Marchetti SB, Egeland L, Mask RA, Eager T, Howell B (2010) Forest ecology and management effects and etiology of sudden aspen decline in Southwestern Colorado, USA. For Ecol Manage 260(5):638–648. https://doi.org/10.1016/j.foreco.2010.05.020

Wulder MA, Dymond CC, White JC, Leckie DG, Carroll AL (2005) Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. For Ecol Manage 221:27–41

Zas R, Björklund N, Sampedro L, Hellqvist C, Karlsson B, Jansson S, Nordlander G (2017) Genetic variation in resistance of Norway spruce seedlings to damage by the pine weevil *Hylobius abietis*. Tree Genet Genomes 13:12. https://doi.org/10.1007/s11295-017-1193-1

Chapter 21
Forest Health in the Anthropocene

Allan L. Carroll

21.1 Introduction

Forests cover approximately one third of Earth's terrestrial surface (FAO and UNEP 2020). They provide a wide range of vital environmental and socioeconomic benefits to all people in the form of ecosystem services. These services include fibre, fuel, non-timber forest products, biodiversity, carbon sequestration, soil and water protection and socio-cultural values (Shvidenko et al. 2005; Brandt et al. 2013; Sing et al. 2017). As the global population rises, the demand for ecosystem services has increased while the capacity of forests to deliver them has declined due to high rates of deforestation (Carpenter et al. 2009; Seidl et al. 2016; FAO and UNEP 2020), and increased rates of disturbance (Johnstone et al. 2016; Seidl et al. 2017). The capacity to quantify the health of forests and assess their ability to sustain ecosystem services into the future has become a fundamental challenge to resource managers in a rapidly changing world.

All forests are adapted in some way to disturbance events that alter ecosystem processes [(White and Pickett 1985; Turner 2010;) see Box 21.1 for definitions]. Following disturbance, forest ecosystems will either regenerate or reorganize. If an ecosystem is resistant to disturbance and returns to a similar pre-disturbance state, it is considered resilient (Holling 1973; Gunderson 2000; Folke et al. 2004; Scheffer 2009). If instead the disturbed ecosystem is sufficiently changed that it regenerates to a different state (e.g. a forest becomes a grassland; Fig. 21.1), then it has undergone a regime shift (Folke et al. 2004; Scheffer 2009; Allen et al. 2016; Johnstone et al. 2016). Relationships between forms of disturbance and the probability of a regime shift are highly non-linear and characterized by thresholds where a relatively small

A. L. Carroll (✉)

Department of Forest & Conservation Sciences, University of British Columbia, Vancouver, BC, Canada
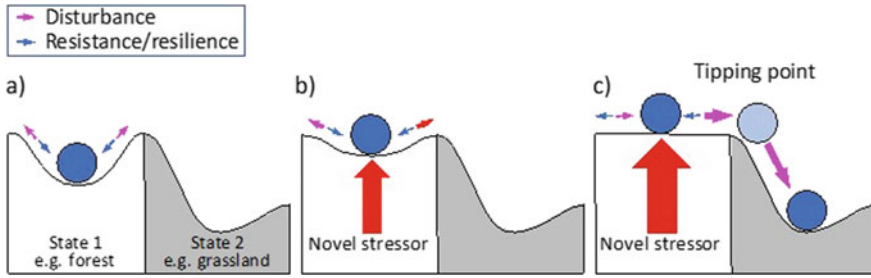
e-mail: allan.carroll@ubc.ca

Fig. 21.1 Conventional cup-and-ball model of ecosystem resilience (Lamothe et al. 2019). The ball represents the current ecosystem, the valleys indicate the possible ecosystem states [e.g. forests (white region) and grasslands (grey region)] and the weight of the arrows indicates the relative strength of interactions. **a)** Forests are resistant and resilient to disturbance where ecosystem processes (blue arrows) maintain them in or return them to their original state following perturbation (pink arrows). **b)** Forests are less resistant and resilient to disturbance due to alteration of ecosystem processes by a novel stressor (red arrow) such as climate change and are therefore less likely to return to their original state following perturbation. **c)** Forests have lost resistance and resilience due to a novel stressor and disturbance has perturbed them beyond their original state to a tipping point where they undergo a regime shift and rapidly reorganize into a new ecosystem

change may lead to a large shift in the state of an ecosystem (Scheffer et al. 2001)—a process known as a tipping point (Brook et al. 2013; Reyer et al. 2015). Over large spatial scales and long time spans, and without significant human intervention, disturbances tend to recur within a natural range of variability (Landres et al.1999). At these scales the characteristics of disturbances together with their return intervals make up a disturbance regime (Turner 2010). Whereas disturbance instigates processes of ecosystem renewal (White and Pickett 1985; Thom et al. 2016), disturbance regimes generate diverse landscapes (Turner 2010; Turner and Gardner 2015; Thom and Seidl 2016).

Box 21.1 Terms and definitions associated with forest ecosystem health

Term	Definition
Disturbance	Any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment (White and Pickett 1985)
Natural range of variability	The ecological conditions, and the spatial and temporal variation in these conditions, that are relatively unaffected by people, within a period of time and geographical area appropriate to an expressed goal (Landres et al. 1999)

(continued)

(continued)

Term	Definition
Disturbance regime	The spatial and temporal dynamics of disturbances that include spatial distribution, frequency, return interval, rotation period, size, intensity, and severity (Turner 2010)
Resistance	The influence of structure and composition on the severity of disturbance (DeRose and Long 2014)
Resilience	The ability of an ecosystem to absorb disturbances and re-organize under change to maintain similar functioning and structure (Scheffer 2009)
Tipping point	A threshold at which a small change in conditions leads to a strong change in the state of a system (Brook et al. 2013)
Regime shift	A rapid modification of ecosystem organization and dynamics with prolonged consequences (Scheffer and Carpenter 2003)

Sustainable extraction of services from forests is contingent upon ecosystems that are resistant and resilient to disturbance (Seidl et al. 2016; Grimm et al. 2016). However, forests around the world are increasingly forced to contend with anthropogenic stressors that influence disturbances both directly via fragmentation, pollution and introduced alien invasive species (Vilà et al. 2010; Paoletti et al. 2010; FAO and UNEP 2020) and indirectly through climate change-mediated alterations to ecosystem processes (Raffa et al. 2009; Seidl et al. 2017; Williams et al. 2019). These novel stressors may reduce the resiliency of forest ecosystems (Fig. 21.1b), increase the probability of abrupt tipping points and regime shifts (Fig. 21.1c), and ultimately threaten the sustainability of ecosystem services. Quantification of the resilience of forest ecosystems and detection of critical changes in condition that may compromise ecosystem service sustainability grows more essential with ongoing global change. In this chapter I will review the concept of forest health, its utility as an indicator of forest ecosystem resistance and resilience to disturbance, and its relevance in an era of extensive global change known as the Anthropocene.

21.2 A Working Definition of Forest Health

The concept of "forest health" as an indicator of ecosystem sustainability is widely accepted; however, its broad adoption has been associated with applications that do not correspond with the term's intent to describe the health of forest ecosystems (Raffa et al. 2009). Thus, a clear and concise definition of forest health is required before it is possible to fully consider its utility and relevance in a changing world. Edmonds et al. (2011) provide a list of eight definitions of forest health. Several

refer to management objectives and human needs, and are considered "utilitarian" (Kolb et al. 1994; Edmonds et al. 2011; Trumbore et al. 2015), while the remainder are based on aspects of ecosystem function and processes. Utilitarian concepts of health are appropriate in agriculture or agroforestry systems that have well-defined management objectives such as the plantation shown in Fig. 21.2a established for the production of fibre. These systems provide valuable services, but they are limited in most aspects of ecological function and are unlikely to be very resistant or resilient to disturbance. Moreover, allowing such systems to behave naturally, for example permitting the growth of competing vegetation, would likely lead to their failure because their goals are to provide socioeconomic benefits often at the expense of ecological processes (Raffa et al. 2009). Based on a utilitarian definition of forest health, the success or failure of a plantation to meet the objective of fibre production would cause it to be deemed a healthy or unhealthy forest, respectively, regardless of ecological condition.

The pitfalls of utilitarian definitions of forest health become more obvious when applied to natural forests. If a disturbance like the native bark beetle outbreak in Fig. 21.2b were to occur in a working forest, the beetle would be considered a pest and the forest unhealthy; however, if the forest was part of a park or protected area,
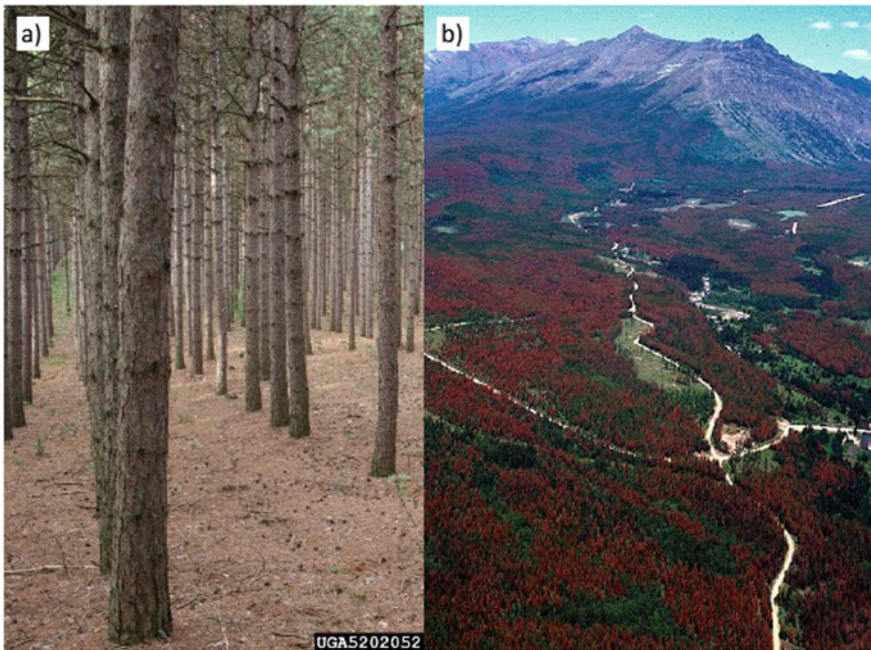

Fig. 21.2 a) A red pine (Pinus resinosa) plantation in central Wisconsin established to produce fibre (*Source* Steven Katovich, Bugwood.org). **b)** A lodgepole pine (*P. contorta* var. *latifolia*) forest in southern British Columbia affected by an outbreak of the mountain pine beetle (*Dendroctonus ponderosae*)

then the beetle would be considered a natural disturbance agent and part of the normal healthy functioning of such an ecosystem (Raffa et al. 2009). Layering of human expectations onto natural forest ecosystems leads to conflicts that preclude the general use of the term "forest health" as an indicator of forest vitality. Processes that make up a functioning forest ecosystem do so independent of human expectations. They include not only the inherent biological, geochemical and physical elements that form the basis of the ecosystem, but also natural disturbances such as windstorms, insect and disease outbreaks and wildfire that arise from interactions among them. All of these processes are essential to resilient ecosystems (Folke et al. 2004; Turner 2010; Johnstone et al. 2016) and should therefore be the basis of a healthy forest. Indeed, several recent studies have emphasized that processes associated with ecosystem resilience must be emphasized when considering forest health, and that health should be measured against ecosystem responses to external drivers and perturbations arising from global change (Raffa et al. 2009; Millar and Stephenson 2015; Trumbore et al. 2015).

Based on the preceding argument, I propose the following definition of forest health that is free from human values and expectations:

> Forests are healthy when their underlying ecological processes operate within a natural range of variability so that on any temporal or spatial scale they are resistant and resilient to disturbance.

It is important to note that this definition is not intended to imply that management of forests toward objectives associated with human values should be abandoned in favour of natural ecological processes. Indeed, careful management of both natural and planted forests can deliver products and services while maintaining ecosystem function (Brandt et al. 2013; Gauthier et al. 2015; Trumbore et al. 2015; Wingfield et al. 2015; Pohjanmies et al. 2017). Instead, restricting the definition of forest health to ecosystem processes allows assessments of the potential of forests (natural, planted or combinations) to remain resilient and provide services in an era of global change.

21.3   Forest Health:From Stands to Landscapes

Since forest health has been defined in terms of resistance and resilience to disturbance, the processes of disturbance and how they interact with ecosystems must be considered in detail. Forest disturbances comprise discrete events that can be manmade (e.g. harvesting or land clearing) or natural. Natural disturbances are either biotic, such as insect or pathogen outbreaks, or abiotic such as wildfires, windstorms, floods, avalanches and volcanic eruptions. By definition, disturbances can operate at spatial scales ranging from individual trees to entire landscapes. However, from the perspective of forest health, a stand[1] is the finest scale at which disturbance will

---

[1] Defined as an area of forest or woodland whose structure or composition is different from adjacent areas (Lindenmayer and Franklin 2002).

be considered because the stand (i) is the fundamental unit of forest management programs, and (ii) it captures key processes associated with ecosystem resilience (McElhinny et al. 2005). The broadest scale of consideration will be the forest landscape which is simply defined as multiple sets of stands that cover an area ranging from hundreds to tens of thousands of hectares (Lindenmayer and Franklin 2002).

21.3.1 Health of Forest Stands

At the scale of a forest stand, the outcome of a disturbance event, and the potential for an ecosystem to either regenerate or reorganize, is a result of complex interactions among disturbance type, severity, structure and composition, and topography of the stand in question (White and Jentsch 2001). Abiotic disturbances such as fire can cause the direct mortality of the majority of plants and animals in an individual stand depending on its severity (Turner et al. 1998). If a fire results in destruction of propagules from the original stand (e.g. a seed bank), then the reduced likelihood of regeneration to an equivalent pre-disturbance state means that the stand was neither resistant to disturbance nor resilient, and therefore unhealthy prior to being disturbed. In contrast, biotic disturbance by an insect defoliator may not directly cause the mortality of any component of a stand, but simply alter the competitive advantage of dominant trees within the overstory leading to a change in canopy composition (Cooke et al. 2007). In this case the stand was largely resistant and resilient to the disturbance, and therefore healthy. Between these extremes, disturbance by both abiotic and biotic agents can be less or more severe, respectively. The severity continuum is further influenced by stand structure and composition. A young stand, or one with a low density of trees, may comprise insufficient fuels to support a high-severity fire (Turner et al. 1994) allowing the stand to regenerate and remain resilient. Similarly, stands without suitable and susceptible host-tree species would be completely resistant to an outbreak of a specialist pathogen or insect disturbance agent (Jactel et al. 2017). Lastly, topographical features of a stand, such as slope and aspect, may influence the severity of both abiotic and biotic disturbances (White and Jentsch 2001) thereby affecting the health of a given stand.

The resilience and health of stands is also potentially influenced by biological legacies that persist through the disturbance event such as surviving trees, seedbanks and/or other below ground organs (Seidl et al. 2014; Johnstone et al. 2016). Given that forest ecosystems have evolved with disturbance, species within them may also display long-term biological legacies in the form of adaptive traits that improve their resistance and/or resilience (Keeley et al. 2011). For example, cone serotiny (the release of seeds in response to an environmental trigger) in some *Pinus* species facilitates the dissemination of seeds immediately following a stand-replacing fire, thus ensuring regeneration of a similar pre-disturbance ecosystem (Turner et al. 1998). Alternatively, many tree species resist disturbance by insect herbivores through adaptations that allow them tolerate tissue loss such as increased photosynthetic and

growth rates, and reallocation of stored resources (Strauss and Agrawal 1999). Similarly, following high-severity fires *Eucalyptus* species resprout epicormically from suppressed, dormant buds along their boles and replace stand canopies within a year of disturbance (Keeley et al. 2011).

21.3.2 Health of Forest Landscapes

While the same disturbances that affect stands will affect landscapes, their relevance to resiliency and forest health may change as spatial and temporal scales increase. For example, disturbance that results in the local destruction of propagules, as with our example of fire above, may lead to the conclusion that a stand was unhealthy prior to fire. But if the stand is situated among other stands (i.e. in a landscape) capable of dispersing seeds into the disturbed area, then regeneration is possible and resiliency is likely. In contrast, local eruption of an aggressive bark beetle population may cause the mortality of a relatively small proportion of mature trees in a mixed species stand, leaving it largely intact. But if surrounding stands contain susceptible host trees the eruption may propagate over the landscape causing extensive tree mortality and threatening ecological processes such as biodiversity and carbon sequestration (Kurz et al. 2008; Raffa et al. 2008).

Disturbance creates gaps in vegetation and alters available light and nutrients, initiating secondary succession within the openings (White and Pickett 1985; White and Jentsch 2001; Turner and Gardner 2015). Variation in these processes will, over time, produce a mosaic of stands across a landscape in different states of regeneration or reorganization (Fig. 21.3). Although the impacts of disturbance may be scale dependent, some forms of disturbance to stands such as that caused by fire or insects can have long-term, persistent impacts on species, communities and ecosystems (White and Jentsch 2001) as a consequence of the biological legacies described above. These forms of disturbance have been referred to as key structuring processes that dominate the formation of patterns over spatial scales of hundreds of metres to hundreds of kilometers (Holling 1992), leading to heterogeneous landscapes. The resultant heterogeneity will influence interactions and exchanges among stands, and ultimately the biotic and abiotic processes associated with forest health at the landscape scale (Turner 1989; Krawchuk et al. 2020).

Heterogeneity influences the resistance of forest landscapes to disturbance through impacts on the susceptibility of stands and the capacity for disturbances to spread within landscapes (Turner and Gardner 2015; Krawchuk et al. 2020). Tree species composition, physiological condition, age and climatic conditions are well known factors that influence the susceptibility of forest stands within a landscape to biotic disturbances by insects and pathogens (Cooke et al. 2007; Raffa et al. 2008; Jactel et al. 2017). The susceptibility of stands to abiotic disturbances will also vary across forested landscapes. For example, areas that are more exposed (edges, gaps, ridgelines) will suffer more windthrow, and drier regions (south-facing slopes, valley
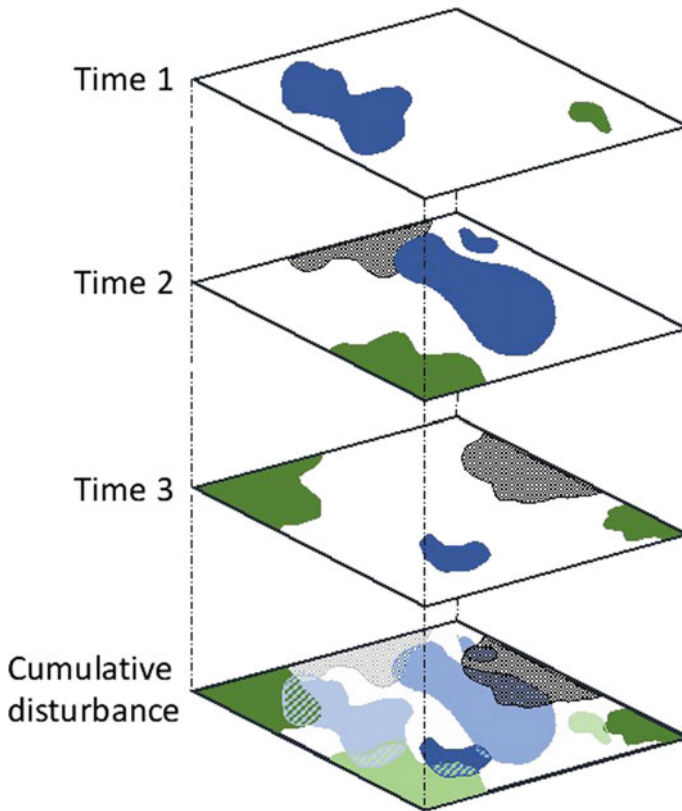
Fig. 21.3 Representation of multiple disturbances acting on the same landscape through time and cumulatively. Colour and pattern indicate different processes, darker shading in the cumulative landscape indicates more recent events. Modified from Parker and Pickett (1998)

bottoms) are more conducive to fire (Turner and Gardner 2015). The spread of disturbances through landscapes may also be impeded by heterogeneity. For example, the distribution of susceptible stands in a landscape will affect the ability of bark beetles to traverse it (Barclay et al. 2005; Raffa et al. 2008). Similarly, low- and moderate-severity wildfires in coniferous forests may be constrained by natural fire breaks and young stands (Turner et al. 1994; Turner and Gardner 2015). Due to the influence of landscape heterogeneity on disturbance susceptibility and spread, even extensive, potentially homogenizing disturbances such as large wildfires will perpetuate further heterogeneity (Turner et al. 1994; Turner 2010; Turner and Gardner 2015). Consider the landscape in Fig. 21.4. The disturbed area within the fire boundary contains areas of varying size with fire severities ranging from none to severe. Such a landscape may be considered resilient and healthy due to the increased probability that areas of severe disturbance can recruit key species to maintain ecological processes from nearby intact areas (Loreau et al. 2001; Krawchuk et al. 2020). By contrast, the
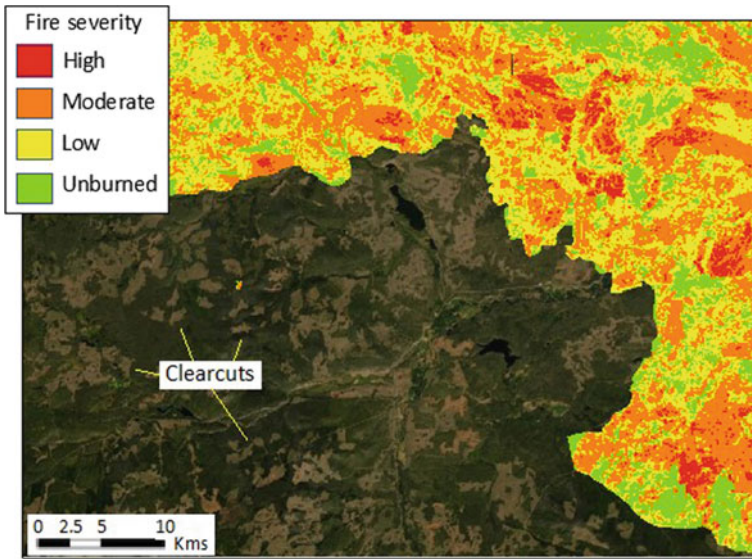
Fig. 21.4 Satellite image of a working forest in central British Columbia, Canada, and adjacent area that burned in a wildfire in 2017. Note the size, distribution and varying severity of the patches disturbed by fire as compared to the clearcuts in the unaffected forest. *Source* ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGrid, IGN, and the GIS User Community

unburned portion of the landscape in Fig. 21.4 has been disturbed by more regular clear-cut harvesting and is relatively less heterogeneous. Maintenance of heterogeneity over landscapes provides "spatial insurance" for healthy ecosystem function by facilitating spatial exchanges among local systems (Loreau et al. 2003).

Over long time-spans patterns of forest disturbance (i.e. disturbance regimes) become apparent with distinct distributions of type, severity, frequency and size (White and Jentsch 2001; Turner 2010; Turner and Gardner 2015). In the absence of anthropogenic alterations, disturbance regimes function within an historic or natural range of variability that can be used to represent the envelope of possible ecosystem conditions over a landscape (Landres et al. 1999). Implicit within the concept of a natural range of variability are the assumptions that ecosystems are dynamic and their responses to change are represented by past variability, and that they have a range of conditions within which they are self-sustaining, beyond which they are not (Keane et al. 2009). Thus, historical conditions can serve as a proxy for forest health (Swetnam et al. 1999) where the resilience of ecosystems is considered in the context of the type, severity, frequency, size, spatial distribution, and return intervals of disturbance. Deviation of disturbance processes within a forest landscape beyond the natural range of variability would threaten its resilience and health.

21.4   Forest Health and Global Change

Global change refers to the independent and interacting effects of anthropogenic stressors on ecosystems at a planetary scale. The primary drivers of global change affecting forests are climate change, land-use change and biotic invasions (Tylianakis et al. 2008). Impacts by these broad stressors on forests can be very complex and sometimes difficult to distinguish from natural variability. Given that the definition of a healthy forest defined above is derived from the processes of disturbance, resistance and resilience, I will examine the interactions of global change drivers with each process in turn using a range of recent examples. My emphasis will be on impacts by novel stressors that perturb forests beyond their natural range of variability (see Fig. 21.1). It is important to note that interactions seldom operate in isolation, and so I will also consider interdependencies for which there is documented evidence and acknowledge that many more interactions are likely at work. Finally, while most examples originate from the northern hemisphere, this is simply a byproduct of available data. The concepts they illustrate are relevant around the world.

21.4.1   Climate Change

Climate change refers to both global warming caused by human emissions of greenhouse gases and the resultant large-scale shifts in weather patterns and extremes. Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia (IPCC 2014). Increasingly, impacts to natural and human systems have been documented on all continents and across the oceans.

21.4.1.1   Disturbance Versus Climate Change

Changing the tempo, intensity, or spatial attributes of disturbance can alter disturbance regimes (Turner 2010; Johnstone et al. 2016; Seidl et al. 2017). As discussed above, when a regime has been modified beyond its natural range of variability then forest landscapes may no longer be resistant and/or resilient, and their health will have been compromised. Perhaps the greatest impact that climate change will have on forest ecosystems in the coming decades will arise from altered disturbance regimes (Lindner et al. 2010). Indeed, many forms of disturbance have already been influenced by climate change (Seidl et al. 2011, 2017). Among the most significant forms of disturbance affected to date are insect outbreaks and wildfire.

Biotic disturbances, primarily caused by insects, affect almost 44 million ha of forests in the northern hemisphere each year (Kautz et al. 2017). Insects are ectothermic, and therefore highly sensitive to changing climate. Not surprisingly, climate change has been implicated in alterations to many aspects of the spatial and

temporal dynamics of forest insects and their potential to cause disturbance. These alterations include shortened life cycle durations (Berg et al. 2006; Choi et al. 2011), increased thermally benign habitats (Carroll et al. 2004; Battisti et al. 2005; Jepsen et al. 2008), enhanced seasonal synchrony among trophic levels and/or the environment (Logan and Powell 2001; Jepsen et al. 2011) and reduced mortality from natural enemies (Stireman et al. 2005; Menéndez et al. 2008). The predominant outcome of these altered dynamics has been a general increase in the rate of biotic disturbance (Kautz et al. 2017; Seidl et al. 2017) potentially leading to modified disturbance regimes.

Despite the general perception that wildfires are increasing in severity around the world, evidence suggests that there is actually less fire in the global landscape today than centuries ago (Doerr and Santín 2016). That said, there are regions where disturbance by wildfire has increased, particularly in western North America. These increases have been attributed to warming-induced changes in atmospheric aridity leading to elevated evaporative demand and reduced fuel moisture, snowpack, and summer precipitation frequency (Abatzoglou and Williams 2016; Williams et al. 2019). Between 1972 and 2018, the area burned in California increased by over 400% (Williams et al. 2019), and virtually all projections based on climate scenarios suggest wildfire potential will continue to rise across western North America (Liu et al. 2010; Jolly et al. 2015). Increased rates of disturbance by fire beyond historic levels raise uncertainties regarding the capacity for forest ecosystem to remain healthy (Turner 2010; Kelly et al. 2013; Millar and Stephenson 2015; Coop et al. 2020).

Interactions among disturbance agents are a major component of disturbance regimes that create heterogeneous, resistant and resilient landscapes (see Fig. 21.3). However, increasing disturbance activity under climate change also means an increasing propensity for disturbance interactions, potentially exacerbating their severity (Buma 2015). In a review and synthesis of climate change effects on important abiotic and biotic disturbances, Seidl et al. (2017) found that links between an initial abiotic agent and subsequent biotic disturbances, especially by bark beetles in conifer forests, were particularly strong and led to amplification of disturbance in the majority of interactions. Bark beetle outbreaks generally arise following an acute pulse of defensively impaired trees that facilitate rapid population increases (Raffa et al. 2008, 2015). This resource pulse is often a result of an initial abiotic disturbance such as a wind storm (Kausrud et al. 2012), wildfire (Hood and Bentz 2007), or drought (Seidl et al. 2016a, b). These interactions can lead to the mortality of trees over many millions of hectares (Raffa et al. 2008). Disturbances at these scales are of particular concern since they are very likely to exceed natural ranges of variation.

21.4.1.2   Resistance Versus Climate Change

Rising temperatures have amplified drought-induced stress in forests around the world (Young et al. 2017; Stephens et al. 2018) and have affected the capacity of ecosystems to resist disturbance. This aspect of climate change is most evident in

interactions of forest ecosystems with phloem-feeding insects such as the bark beetles whose attack and colonization success are constrained by tree defenses that are sensitive to water availability (Raffa et al. 2015; Marini et al. 2017). Many conifers close stomata to protect xylem cells from cavitation during drought, reducing photosynthesis to near zero (Koepke and Kolb 2013). However, production and deployment of defensive resin is reduced under conditions of limited photosynthesis, thus lowering tree resistance to bark beetle attacks during droughts (Raffa et al. 2015).

Climate change-exacerbated droughts have also affected forest resistance to abiotic disturbances such as wildfire. Drought not only causes increased amounts of fuels in forests in the form of dead wood, it also reduces the moisture content within those fuels and alters the ratio of dead to live fuels within the canopy of living trees, thus reducing the resistance of some forests to fire and facilitating larger, more severe fires (Stephens et al. 2018; Nolan et al. 2020).

21.4.1.3   Resilience Versus Climate Change

The structural and functional changes in forests in response to disturbance may compromise their capacity to recover in a warming environment. Evidence is accumulating that forest ecosystem resilience may be affected by climate change-exacerbated wildfires. In the western region of the North American boreal forest, drier and warmer weather associated with climate change has decreased the resilience of ecosystems by reducing the interval between wildfires leading to altered patterns of regeneration (Whitman et al. 2019; Coop et al. 2020).

Similarly, in the western US, increasingly unfavorable post-fire growing conditions due to a changing climate have compromised ecosystem resilience by reducing seedling establishment and increasing regeneration failures (Harvey et al. 2016; Stevens-Rumann et al. 2018; Davis et al. 2019; Coop et al. 2020). These impacts comprise an abrupt tipping point given that fire has killed the adult trees that could have persisted in the warmer conditions, but since those conditions are no longer suitable for seedling establishment and survival, ecosystems cannot return to similar pre-disturbance conditions (Davis et al. 2019).

21.4.2   Land-Use Change

Land-use change typically refers to the permanent conversion of forests as opposed to temporary losses from wildfires or harvesting. Where land-use change leads to loss of forest, it results in disturbance well beyond the natural range of variability and complete negation of forest health. This form of global change is a significant impact to forested landscapes. Deforestation through land-use change is responsible for over one-quarter of forest loss around the world (Curtis et al. 2018). By contrast, partial land-use changes, also known as forest degradation, may be less severe and involve retention of some ecological processes (Ghazoul et al. 2015; Ghazoul and Chazdon

2017), allowing consideration of forest health. Since partial land-use changes are associated with diminished or constrained ecological function within forests, examples are broad and include extraction of non-timber forest products, collection of fuel wood, free-range livestock grazing, shifting cultivation, selective logging, urban encroachment and wildfire suppression (Thompson et al. 2013). These activities have the potential to alter all aspects of forest health.

21.4.2.1   Disturbance Versus Land-Use Change

Partial land-use changes can significantly alter the behaviour and characteristics of disturbances, especially abiotic disturbance. Wildfires depend on the coincidence of dry weather, available fuel and ignition sources (Jolly et al. 2015). As outlined above, weather conditions conducive to fire have increased due to climate change-related drought in many regions. In western North America, land-use changes have also affected the remaining two requirements for severe wildfires. The legacy of human settlement and fire suppression has contributed to increased fuel loads in forests (Higuera et al. 2015; Parks et al. 2015). Moreover, growing populations and urban encroachment have resulted in increased frequency and type of human-caused ignitions (Balch et al. 2017; Radeloff et al. 2018). Thus, land-use changes have further exacerbated the impacts of climate change in terms of fire severity, particularly in the western US as evidenced by recent record-breaking fire seasons.

21.4.2.2   Resistance Versus Land-Use Change

In many cases, partial land-use changes have reduced the resistance of forests to disturbances by constraining or removing critical ecosystem functions. For example, widespread fire suppression in biomes adapted to frequent wildfires can severely compromise resistance to both abiotic and biotic disturbances. In western Canada, aggressive fire suppression over the past century allowed large areas of pine-dominated forests to age to the point of becoming highly susceptible (i.e. less resistant) to the mountain pine beetle (Taylor and Carroll 2004), leading to a "hyper-epidemic" that reached an order of magnitude greater extent and severity than any previously recorded (Sambaraju et al. 2019).

Wind is one of the most important abiotic forest disturbances in many parts of the world (Seidl et al. 2017). In tropical forests prone to cyclones and hurricanes, altered forest structure (increased gaps, edges) and shifts in plant species composition as a result of forest fragmentation reduce the resistance of forests to storm damage (Laurance and Curran 2008). Similarly, in the Norway spruce forests of Europe, resistance to wind disturbances is compromised by fragmentation (Zeng et al. 2009). In these forests wind disturbance is further amplified by outbreaks of the European spruce beetle that erupt from freshly broken or uprooted trees and spread into intact forests (Stadelmann et al. 2014).

21.4.2.3 Resilience Versus Land-Use Change

Reduced resilience of forest ecosystems associated with partial land-use change is common when the change interrupts biological legacies and impairs regeneration. For example, repeated burning of forested areas to promote livestock grazing in the Amazon has led to reduced seed availability and seedling recruitment and subsequent reorganization to shrub-dominated landscapes (Mesquita et al. 2015). Similarly, the resilience of some old-growth eucalypt forests in Australia have been diminished by clear cut logging that increases both fine fuels and the prevalence of young densely stocked stands that together support elevated fire severity compromising the capacity for systems to regenerate to equivalent pre-logging conditions (Lindenmayer et al. 2011).

21.4.3   Biotic Invasions

Biological invasions have become a defining feature of the Anthropocene (Lewis and Maslin 2015). Dramatic increases in human transport and commerce have increased the rate of introductions of non-native species into virtually all habitats around the world. Although most species introduced into new habitats will not survive, some will establish and persist. A small percentage of those that persist can become invasive where they proliferate and spread to the detriment of the environment (Mack et al. 2000; Aukema et al. 2010). Invasive species can affect all ecological processes within forests causing altered diversity, nutrient cycling, succession, and frequency and intensity of wildfires (Kenis et al, 2009; Liebhold et al. 2017). Non-native organisms from nearly every taxon have been introduced into forests; however, insects represent the most diverse group of invaders (Brockerhoff and Liebhold 2017; Liebhold et al. 2017). Thus, the examples discussed below will be mostly derived from invasive forest insects.

21.4.3.1 Disturbance Versus Biotic Invasions

The most apparent impact of biotic invasions within forest ecosystems involves altered disturbance rates as a result of direct tree mortality caused by the invasive organisms. There are many examples of these types of disturbances (Gandhi and Herms 2009; Kenis et al. 2009; Brockerhoff and Liebhold 2017). Among the most severe are the hemlock woolly adelgid and the emerald ash borer. The hemlock woolly adelgid, a sap feeder, was accidentally introduced from Japan to the eastern US during the early decades of the last century (Brockerhoff and Liebhold 2017). It has caused extensive mortality of eastern hemlock, causing its decline as a dominant forest species throughout eastern North America (Morin and Liebhold 2015). More recently, the emerald ash borer was introduced from north-eastern Asia to both North America and western Russia (Herms and McCullough 2014). Since its arrival it has

caused extensive mortality and eliminated the majority of ash trees (*Fraxinus* spp.) within the areas it has invaded (Straw et al. 2013; Herms and McCullough 2014; Morin et al. 2017).

Disturbances associated with biotic invasions will potentially worsen under climate change. Hellman et al. (2008) discuss the potential impacts of a warming environment on invasive species. Three impacts in particular are relevant to forest disturbance; (i) altered climatic constraints on invasive species, (ii) altered distribution of existing invasive species, and (iii) altered impact of existing invasive species. The sum of these impacts implies a general increase in thermally benign habitats available to invasive species that may lead to higher rates of disturbances in forests as the climate continues to warm. Indeed, the number of established alien species is projected to continue increasing through the current century (Seebens et al. 2021).

21.4.3.2 Resistance Versus Biotic Invasions

The term biotic resistance is used to describe the ability of communities to resist invasive species. In general, forests tend to be more resistant to invasions than other terrestrial systems due to their inherently high diversity and the resultant interactions of introduced organisms with native competitors, predators, etc. (Iannone et al. 2016; Nunez-Mir et al. 2017). However, when invasive species cause extensive forest disturbances, it is most often a consequence of an insufficient or inadequate response on the part of trees to defend themselves from herbivores (Brockerhoff and Liebhold 2017). This is referred to as the defense-free space hypothesis in which population growth and spread of an invader is facilitated by low resistance of evolutionarily naïve host plants (Gandhi and Herms 2009). Defense-free space has been implicated in the exacerbated impacts of many invasive forest insects and pathogens including hemlock woolly adelgid and emerald ash borer mentioned above (Showalter et al. 2018).

The concept of defense-free space is not confined to interactions of non-native organisms with forest ecosystems. Native herbivorous insects are often constrained by climate to a portion of the range of their host trees. As discussed above, a warming environment has been associated with increases in the availability of thermally benign habitats for several insect species, facilitating an expansion of ranges into evolutionarily naïve populations and species of host trees (Burke et al. 2017). Due to an insufficiently evolved defensive response, the resistance of naïve host tree populations and species to native climate migrants is inadequate to prevent severe disturbance (Cudmore et al. 2010; Raffa et al. 2013; Clark et al. 2014). This phenomenon is best exemplified by the recent expansion of the mountain pine beetle across the Rocky Mountains of North American and invasion of the transcontinental boreal forest (Cooke and Carroll 2017).

21.4.3.3   Resilience Versus Biotic Invasions

Biotic invasions that result in extensive disturbances to evolutionarily naïve forests are by definition beyond the range of historic variability. Hence, impacts to the processes associated with ecosystem resilience are often extreme and forests are forced to reorganize. Many examples exist of drastically altered ecosystems as a consequence of biotic invasion, but perhaps the best known is that associated with a fungal pathogen, the chestnut blight, accidentally introduced from Asia into North America in the early 1900s (Griffin 1986). The resultant devastation of the American chestnut by the fungus represents one of the greatest recorded changes to a forest biome caused by an introduced organism (Liebhold et al. 1995). Within a relatively short period of its introduction, the pathogen spread and functionally eliminated the American chestnut through most of its range. The loss of chestnut trees throughout eastern North America has had spectacular and long-term effects on forest ecosystems including reorganization to oak-dominated overstories, altered disturbance regimes and loss of wildlife habitat.

21.5   Forest Health in Practice

This chapter has defined forest health, outlined its constituent components across spatial and temporal scales, and reviewed the impacts of global change on each. How then are changes in forest health detected and how can forests be managed to allow sustainable extraction of ecosystem services? The foundation of the definition of a healthy forest is that its ecological processes operate within an envelope of possible ecosystem conditions. This concept of a natural range of variability (Landres et al. 1999) provides a framework for understanding the ecological context of a forest and in evaluating changes in its health.

Quantifying natural variability in forests requires information on the ecological processes and conditions of interest and their variation through time and space. This information is obtained from studies in the fields of dendroecology, dendroclimatology, palynology, landscape ecology and remote sensing that provide measurements over a sufficiently long time period and spatial extent so that meaningful information can be gained about changes in populations, ecosystem structures, disturbance frequencies, process rates, trends, periodicities, and other dynamical behaviors (Swetnam et al. 1999). Application of the concept of natural range of variability to ecosystem management is based on the following premises as reviewed by Landres et al. (1999):

- contemporary anthropogenic change may diminish the viability of many species that are adapted to past or historical conditions and processes;
- approximating historical conditions will sustain the viability of diverse species, even for those for which we have limited information;

- natural variability is a reference for evaluating the influence of anthropogenic change in ecological systems at local and shorter time scales;
- natural variability encompasses the dynamic ecological processes that drive both spatial and temporal variation in ecological systems, as well as the influence of this variation on evolution and biological diversity;
- disturbances have a strong and lasting influence on species, communities, and ecosystems;
- spatial heterogeneity is an integral component of ecological systems that is positively related to biodiversity, and resistance and resilience to disturbance.

Although difficult to generate, considerable information regarding the natural range of variability of ecological processes within many forest types has been amassed in recent decades (Keane et al. 2009). Indeed, it is now widely recognized that forest management should seek to emulate the natural range of variability of forests to maintain biodiversity and ecological function (Drever et al. 2006; Keane et al. 2009; Čada et al. 2020; Donato et al. 2020). This recognition has stimulated efforts to minimize differences between managed and natural forests by, for example, modifying harvesting practices to generate spatial and temporal patterns consistent with historical disturbance regimes (Bergeron et al. 2002; Harvey et al. 2002; Kuuluvainen and Grenfell 2012; Leclerc et al. 2021).

Consideration of disturbance, resistance and resilience within the context of natural range of variability may at first seem overly simplistic since it assumes that the record of historical conditions must reflect the range of possible conditions for future landscapes, thus ignoring the potential impacts of global change. However, determination of the natural range of variability of forest ecosystems necessarily captures large variations in the conditions of past centuries (Swetnam et al. 1999), and therefore it remains relevant even when faced with anthropogenic change. Moreover, the potential impacts of global change may be buffered by aspects of forest health. Landscape heterogeneity is directly related to species diversity (Tews et al. 2004; Fahrig et al. 2011) and diversity improves resistance and resilience to disturbance by virtue of spatial exchanges among local systems in heterogeneous landscapes (Loreau et al. 2003; Brockerhoff et al. 2017; Krawchuk et al. 2020). Thus, a forest type with higher species diversity will be healthier than an otherwise equivalent, but depauperate one, and better able to withstand novel stressors. Species diversity can be quantified at each spatial scale relevant to forest health using the concept of α-, β- and γ-diversity (Whittaker 1972; Veech et al. 2002), where α-diversity refers to species diversity within stands, β-diversity refers to species diversity among stands in a landscape, and γ-diversity is the total species diversity of the biome (i.e. sets of landscapes comprising distinct biological communities that have formed in response to a shared physical climate).

Indicators of forest health vary from stands to biomes and can be expressed in terms of each of our components of forest health—disturbance, resistance and resilience (Fig. 21.5). At the finest scale, a healthy stand is one where the type, severity and frequency of any disturbance falls within the range of natural variability. The capacity for a stand to respond to disturbance and remain within the historic range

of ecosystem conditions (i.e. avoid tipping points and regime shifts) is contingent upon its inherent resistance and resilience. Since resistance and resilience increase with increasing diversity, then at any point in time, a stand will be healthier with greater α-diversity relative to equivalent stands at similar successional stages. And as discussed above, stands are further considered healthy if following disturbance, they successfully regenerate (naturally or by planting) along a successional trajectory that will return them to a functionally equivalent pre-disturbance state. Similarly, indicators of forest health at the scale of landscapes comprise disturbance regimes (type, severity, frequency, size and return interval) that remain within the natural range of variability, high relative β-diversity and heterogeneous structures derived from diverse seral stages with high connectivity. And finally, forest biomes will be healthy when disturbance regimes within constituent landscapes remain within the natural range of variability, there is high absolute γ -diversity and all constituent landscapes persist through time (Trumbore et al. 2015).

21.5.1   Forest Health Monitoring

Given that the processes of forest health vary across scales (Fig. 21.5), forest health monitoring programs must collect and synthesize data within and among scales to support managers, decision makers, and politicians in their decisions regarding forest management. Within stands, health conditions are often measured directly from individual forest inventory plots where species diversity, and the status of trees, vegetation, soils and other ecosystem properties are quantified. These data may be augmented with high-resolution remote-sensing techniques such RADAR or LiDAR which have the potential to reconstruct forest structures within and below the canopy (Lausch et al. 2017). Data at broader scales can be derived from networks of forest inventory plots (Woodall et al. 2011) and from a wide variety of broad-scale remote sensing techniques (Lausch et al. 2016).

Despite considerable efforts by many countries to develop comprehensive forest health monitoring programs, there still remains some discrepancy between the information required by forest managers and the data that are available for understanding and assessing the complexity of forest health processes (Lausch et al. 2018). Long-term monitoring based on forest inventory plot networks provides valuable information regarding trends in forest health processes (Tkacz et al. 2008; Woodall et al. 2011); however, short-term perturbations that may trigger abrupt nonlinear declines in health are not sufficiently assessed since measurement intervals are often multiple years (Lausch et al. 2017). More recently, integration of forest inventory plot networks with remote sensing tools has facilitated generalization of intensive and expensive ground-based measurements to temporal and spatial scales required by forest managers (McDowell et al. 2015).

Forest health indicators

- *Disturbance*:
  Type, severity, frequency
- *Resistance*:
  Relative **α** diversity
- *Resilience*:
  Regeneration success,
  Successional trajectory

- *Disturbance*:
  Type, severity, frequency,
  size, return interval
- *Resistance*:
  Relative **β** diversity
- *Resilience*:
  Seral diversity, connectivity
  heterogeneity

- *Disturbance*:
  Type, severity, frequency,
  size, return interval
- *Resistance*:
  γ diversity
- *Resilience*:
  Landscape persistence

Stand   Landscape   Biome

Forest health monitoring tools

- Forest inventory plot
- High-resolution remote sensing

- Forest inventory plot network
- Remote sensing

- Remote sensing

Fig. 21.5 Indicators and monitoring tools for forest health at the stand-, landscape- and biome-scale. Indicators are scale dependent, and refer to (i) disturbance (type, severity, frequency, size, return interval) within a natural range of variability, (ii) resistance defined by stand- (**α**) and landscape- (**β**) diversity relative to equivalent stands and landscapes in the biome, or total species diversity (**γ**) in the biome, and (iii) resilience to disturbance defined as the capacity for forests to return to equivalent pre-disturbance states at each scale. Forest health monitoring tools are also scale dependent and range from individual plots in stands to broad-scale remote sensing

21.6 Forest Health Versus Nonconventional Forests

Although planted forests comprise approximately 7% of forests around the world, they account for roughly 70% of industrial wood products (Carle and Homgren 2008). The demand for wood products from plantations has been growing, and so has the area devoted to plantations such that the area of planted forest is likely to double by the end of the century (Brockerhoff et al. 2013). The majority of plantation forests comprise non-native *Pinus*, *Eucalyptus* and *Acacia* species in the southern hemisphere and mostly native species in several northern hemisphere countries (Payn et al. 2015). As the emphasis on plantation forestry has grown, so has the need for assessments of ecosystem health.

As discussed above, the definition of forest health derived from processes of disturbance, resistance and resilience does not necessarily exclude intensively managed

plantations, so how is it applied? Since plantations are largely artificial constructs the concepts of natural range of variability and disturbance regimes are not applicable. Indeed, disturbances are mainly restricted to biotic agents such as insects and pathogens (Wingfield et al. 2015). Further, issues of resilience to disturbance (and associated tipping points and regime shifts) are rendered largely irrelevant since intensive management will lead to immediate investments toward regeneration of any disturbed areas. In contrast, resistance processes that influence the severity of disturbance are vital to forest plantations (Brockerhoff et al. 2013; Wingfield et al. 2015) and provide the basis for the assessment of their health.

Planted forests are typically of a single, non-native species grown primarily for efficient wood production. They tend to be characterised by lower levels of biodiversity than natural and semi-natural forests (Brockerhoff et al. 2008) and they achieve high productivity mainly through intensive pest control efforts or the outright exclusion of pests (Liebhold et al. 2017; Wingfield et al. 2015). When pest impacts do occur, large amounts of damage can result.

Mixed-species forests are more resistant than monocultures to biotic disturbance due to the greater abundance of trophic interactions that regulate biotic disturbance agents (Jactel et al. 2017). Although plantations are normally established as monocultures, they afford an ideal opportunity to create diversity and increase resistance to disturbance given that replanting after harvesting is a frequent and recurrent process (Brockerhoff et al. 2017; Paquette and Messier 2010). Based on the expectation of increasing disturbance in a warmer world (see discussion above), greater resistance to disturbance through creation of mixed-species plantations should offset any short-term costs associated with their establishment.

In light of the capacity for innovative management of intensive plantations to promote diversity and resistance, Brockerhoff et al. (2013) recommend that clearing natural vegetation should be avoided prior to planting, native tree species should be preferred, and where possible mixed-species plantations should be established. Furthermore, in keeping with the expectations of a healthy forest landscape, they recommend the protection and enhancement of remnants of natural vegetation, the creation of mosaics of stand ages and tree species and the establishment of corridors linking habitat patches.

21.7 Conclusions

Increasingly forests are threatened by anthropogenic stressors arising from global change that compromise provisioning of vital ecosystem services. Therefore, the need to promote forest ecosystems that are resistant and resilient to stressors has never been greater. Forests are highly complex and their response to natural and anthropogenic stressors is difficult to quantify. Given an increasing global population, forests cannot and should not be viewed as independent of human influences; however, the capacity to identify the source and impact of natural and anthropogenic stressors is essential for effective forest management intended to foster forest health. A definition of

forest health derived from ecological processes, and independent of human values, facilitates baseline assessments of forest function at all temporal and spatial scales and allows partitioning of the relative impacts of natural and anthropogenic stressors and their interactions. Defining forest health in terms of the processes of disturbance, resistance and resilience within natural ranges of variability allows quantification of the vitality of any forest type in any conceivable state and determine its probability of persistence.

The ability of forests to be resistant and resilient to disturbance is dependent upon species diversity and landscape heterogeneity. Resistant and resilient forests will retain ecological processes and the capacity to deliver ecosystem services. Therefore, management toward healthy forests should seek to maximize relative biodiversity at all scales as much as is practicable. In so doing, we can provide spatial insurance for ecosystem functioning (Loreau et al. 2003) by increasing the probability of robust resistance and resilience in the face of global change.

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. Proc Natl Acad Sci 113:11770–11775

Allen CR, Angeler DG, Cumming GS, Folke C, Twidwell D, Uden DR (2016) Quantifying spatial resilience. J Appl Ecol 53:625–635

Aukema JE, McCullough DG, Holle BV, Liebhold AM, Britton K, Frankel SJ (2010) Historical accumulation of nonindigenous forest pests in the Continental United States. Bioscience 60:886–897

Balch JK, Bradley BA, Abatzoglou JT, Nagy RC, Fusco EJ, Mahood AL (2017) Human-started wildfires expand the fire niche across the United States. Proc Natl Acad Sci 114:2946–2951

Barclay HJ, Li C, Benson L, Taylor S, Shore T (2005) Effects of fire return rates on traversability of lodgepole pine forests for mountain pine beetle (Coleoptera: Scolytidae) and the use of patch metrics to estimate traversability. Can Entomol 137:566–583

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol Appl 15:2084–2096

Berg EE, Henry JD, Fastie CL, Volder ADD, Matsuoka SM (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. For Ecol Manage 227:219–232

Bergeron Y, Leduc A, Harvey B, Gauthier S (2002). Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn 36. https://doi.org/10.14214/sf.553

Brandt JP, Flannigan MD, Maynard DG, Thompson ID, Volney WJA (2013) An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues1. Environ Rev 21:207–226

Brockerhoff EG, Barbaro L, Castagneyrol B, Forrester DI, Gardiner B, González-Olabarria JR et al (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. Biodivers Conserv 26:3005–3035

Brockerhoff EG, Jactel H, Parrotta JA, Ferraz SFB (2013) Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. For Ecol Manage 301:43–50

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925–951

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biol Invasions 19:3141–3159

Brook BW, Ellis EC, Perring MP, Mackay AW, Blomqvist L (2013) Does the terrestrial biosphere have planetary tipping points? Trends Ecol Evol 28:396–401

Buma B (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15

Burke JL, Bohlmann J, Carroll AL (2017) Consequences of distributional asymmetry in a warming environment: invasion of novel forests by the mountain pine beetle. Ecosphere 8:e01778

Čada V, Trotsiuk V, Janda P, Mikoláš M, Bače R, Nagel TA et al (2020) Quantifying natural disturbances using a large-scale dendrochronological reconstruction to guide forest management. Ecol Appl 30. https://doi.org/10.1002/eap.2189

Carle J, Homgren P (2008) Wood from planted forests: a global outlook 2005–2030. For Prod J 58:6–18

Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Díaz S et al (2009) Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. Proc Natl Acad Sci 106:1305–1312

Carroll AL, Taylor SW, Régnière J, Safranyik L (2004). Effects of climate change on range expansion by the mountain Pine Beetle in British Columbia. In: Shore TL, Stone JE Stone (eds) Mountain Pine Beetle symposium: challenges and solutions. Natural Resources Canada, Canadian Forest Service, Victoria, BC, Canada, pp 223–232

Choi WI, Park Y-K, Park Y-S, Ryoo MI, Lee H-P (2011) Changes in voltinism in a pine moth Dendrolimus spectabilis (Lepidoptera: Lasiocampidae) population: implications of climate change. Appl Entomol Zool 46:319–325

Clark EL, Pitt C, Carroll AL, Lindgren BS, Huber DPW (2014) Comparison of lodgepole and jack pine resin chemistry: implications for range expansion by the mountain pine beetle, Dendroctonus ponderosae (Coleoptera: Curculionidae). PeerJ 2:e240

Cooke BJ, Carroll AL (2017) Predicting the risk of mountain pine beetle spread to eastern pine forests: Considering uncertainty in uncertain times. For Ecol Manage 396:11–25

Cooke BJ, Nealis VG, Régnière J (2007) Insect defoliators as periodic disturbances in northern forest ecosystems. In: Johnson EA, Miyanishi K (eds) Plant disturbance ecology: the process and the response. Elsevier Academic Press, Burlington, Mass, USA, pp 487–525

Coop JD, Parks SA, Stevens-Rumann CS, Crausbay SD, Higuera PE, Hurteau MD et al (2020) Wildfire-Driven forest conversion in Western North American landscapes. Bioscience 70:659–673

Cudmore TJ, Björklund N, Carroll AL, Lindgren BS (2010) Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. J Appl Ecol 47:1036–1043

Curtis PG, Slay CM, Harris NL, Tyukavina A, Hansen MC (2018) Classifying drivers of global forest loss. Science 361:1108–1111

Davis KT, Dobrowski SZ, Higuera PE, Holden ZA, Veblen TT, Rother MT et al (2019) Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc Natl Acad Sci 116:201815107

DeRose RJ, Long JN (2014) Resistance and resilience: a conceptual framework for silviculture. For Sci 60:1205–1212

de Mesquita R, C. G., Massoca, P. E. dos S., Jakovac, C. C., Bentos, T. V., & Williamson, G. B. (2015) Amazon rain forest succession: stochasticity or land-use legacy? Bioscience 65:849–861

Doerr SH, Santín C (2016) Global trends in wildfire and its impacts: perceptions versus realities in a changing world. Philosophical transactions of the royal society : Biol Sci 371:20150345

Donato DC, Halofsky JS, Reilly MJ (2020) Corralling a black swan: natural range of variation in a forest landscape driven by rare, extreme events. Ecol Appl 30. https://doi.org/10.1002/eap.2013

Drever CR, Peterson G, Messier C, Bergeron Y, Flannigan M (2006) Can forest management based on natural disturbances maintain ecological resilience? Can J for Res 36:2285–2299

Edmonds RL, Agee JK, Gara RI (2011) Forest health and protection. Waveland Press, Long Grove, IL, USA

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ et al (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14:101–112

FAO, and UNEP (2020) The state of the world's forests 2020. forests, biodiversity and people. Rome: food and agriculture organization of the United Nations and UN Environment Program.

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581

Gandhi KJK, Herms DA (2009) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol Invasions. https://doi.org/10.1007/s10530-009-9627-9

Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG (2015) Boreal forest health and global change. Science 349:819–822

Ghazoul J, Burivalova Z, Garcia-Ulloa J, King LA (2015) Conceptualizing forest degradation. Trends Ecol Evol 30:622–632

Ghazoul J, Chazdon R (2017) Degradation and recovery in changing forest landscapes: a multiscale conceptual framework. Annu Rev Environ Resour 42:161–188

Griffin GJ (1986) Chestnut blight and its control. Horticultural Review 8:291–335

Grimm NB, Groffman P, Staudinger M, Tallis H (2016) Climate change impacts on ecosystems and ecosystem services in the United States: process and prospects for sustained assessment. Clim Change 135:97–109

Gunderson LH (2000) Ecological resilience—in theory and application. Annu Rev Ecol Syst 31:425–439

Harvey BJ, Donato DC, Turner MG (2016) High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob Ecol Biogeogr 25:655–669

Harvey BJ, Leduc A, Gauthier S, Bergeron Y (2002) Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For Ecol Manage 155:369–385

Hellman JJ, Byers JE, Biergarden BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. Conserv Biol 22:534–543

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu Rev Entomol 59:13–30

Higuera PE, Abatzoglou JT, Littell JS, Morgan P (2015) The changing strength and nature of fire-climate relationships in the Northern rocky mountains, U.S.A., 1902–2008. PLOS One, 10:e0127563.

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Holling CS (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. Ecol Monogr 62:447–502

Hood S, Bentz B (2007) Predicting postfire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains. Can J for Res 37:1058–1069

Iannone BV, Potter KM, Hamil K-AD, Huang W, Zhang H, Guo Q et al (2016) Evidence of biotic resistance to invasions in forests of the Eastern USA. Landscape Ecol 31:85–99

IPCC. (2014). Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change, Geneva, Switzerland: IPCC, p 151

Jactel H, Bauhus J, Boberg J, Bonal D, Castagneyrol B, Gardiner B et al (2017) Tree diversity drives forest stand resistance to natural disturbances. Curr For Rep 3:223–243

Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids Operophtera brumata and Epirrita autumnata in subarctic birch forest: evidence of a recent outbreak range expansion. J Anim Ecol 77:257–264

Jepsen JU, Kapari L, Hagen SB, Schott T, Vindstad OPL, Nilssen AC, Ims RA (2011) Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. Glob Change Biol 17:2071–2083

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE et al (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. Nat Commun 6:7537

Kausrud K, Okland B, Skarpaas O, Grégoire J-C, Erbilgin N, Stenseth NC (2012) Population dynamics in changing environments: the case of an eruptive forest pest species. Biol Rev Camb Philos Soc 87:34–51

Kautz M, Meddens AJH, Hall RJ, Arneth A (2017) Biotic disturbances in Northern Hemisphere forests—a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Glob Ecol Biogeogr 26:533–552

Keane RE, Hessburg PF, Landres PB, Swanson FJ (2009) The use of historical range and variability (HRV) in landscape management. For Ecol Manage 258:1025–1037

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci 16:406–411

Kelly R, Chipman ML, Higuera PE, Stefanova I, Brubaker LB, Hu FS (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proc Natl Acad Sci 110:13055–13060

Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré C, Cock MJW et al (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45

Koepke DF, Kolb TE (2013) Species variation in water relations and xylem vulnerability to cavitation at a forest-woodland ecotone. For Sci 59:524–535

Kolb TE, Wagner MR, Covington WW (1994) Utilitarian and ecosystem perspectives: concepts of forest health. J Forest 92:10–15

Krawchuk MA, Meigs GW, Cartwright JM, Coop JD, Davis R, Holz A et al (2020) Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. Front Ecol Environ 18:235–244

Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL et al (2008) Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990

Kuuluvainen T, Grenfell R (2012) Natural disturbance emulation in boreal forest ecosystem management—theories, strategies, and a comparison with conventional even-aged management. Can J for Res 42:1185–1203

Lamothe KA, Somers KM, Jackson DA (2019) Linking the ball-and-cup analogy and ordination trajectories to describe ecosystem stability, resistance, and resilience. Ecosphere 10:e02629

Landres PB, Morgan P, Swanson FJ (1999) Overview of the use of natural variability concepts in managing ecological systems. Ecol Appl 9:1179–1188

Laurance WF, Curran TJ (2008) Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. Austral Ecol 33:399–408

Lausch A, Borg E, Bumberger J, Dietrich P, Heurich M, Huth A et al (2018) Understanding forest health with remote sensing, part III: requirements for a scalable multi-source forest health monitoring network based on data science approaches. Remote Sens 10:1120

Lausch A, Erasmi S, King DJ, Magdon P, Heurich M (2017) Understanding forest health with Rrmote sensing-part II—A review of approaches and data models. Remote Sens 9:129

Lausch A, Erasmi S, King D, Magdon P, Heurich M (2016) Understanding forest health with remote sensing–part I—A review of spectral traits. processes and remote-sensing characteristics. Remote Sens 8:1029

Leclerc M-AF, Daniels LD, Carroll AL (2021) Managing wildlife habitat: complex interactions with biotic and abiotic disturbances. Front Ecol Evol 9:613371

Lewis SL, Maslin MA (2015) Defining the anthropocene. Nature 519:171–180

Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ (2017) Biological invasions in forest ecosystems. Biol Invasions 19:3437–3458

Liebhold AM, MacDonald WL, Bergdahl D, Mastro VC (1995) Invasion by exotic forest pests: a threat to forest ecosystems. Forest Science Monographs 30:1–49

Lindenmayer DB, Hobbs RJ, Likens GE, Krebs CJ, Banks SC (2011) Newly discovered landscape traps produce regime shifts in wet forests. Proc Natl Acad Sci 108:15887–15891

Lindenmayer DB, Franklin JF (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manage 259:698–709

Liu Y, Stanturf J, Goodrick S (2010) Trends in global wildfire potential in a changing climate. For Ecol Manage 259:685–697

Logan JA, Powell JA (2001) Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). Am Entomol 47:160–172

Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. Proc Natl Acad Sci 100:12765–12770

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A et al (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710

Marini L, Okland B, Jönsson AM, Bentz B, Carroll AL, Forster B et al (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography. https://doi.org/10.1111/ecog.02769

McDowell NG, Coops NC, Beck PSA, Chambers JQ, Gangodagamage C, Hicke JA et al (2015) Global satellite monitoring of climate-induced vegetation disturbances. Trends Plant Sci 20:114–123

McElhinny C, Gibbons P, Brack C, Bauhus J (2005) Forest and woodland stand structural complexity: Its definition and measurement. For Ecol Manage 218:1–24

Menéndez R, González-Megías A, Lewis OT, Shaw MR, Thomas CD (2008) Escape from natural enemies during climate-driven range expansion: a case study. Ecological Entomology 33:413–421

Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. Science 349:823–826

Morin RS, Liebhold AM (2015) Invasions by two non-native insects alter regional forest species composition and successional trajectories. For Ecol Manage 341:67–74

Morin RS, Liebhold AM, Pugh SA, Crocker SJ (2017) Regional assessment of emerald ash borer, Agrilus planipennis, impacts in forests of the Eastern United States. Biol Invasions 19:703–711

Nolan RH, Blackman CJ, de Dios VR, Choat B, Medlyn BE, Li X et al (2020) Linking forest flammability and plant vulnerability to drought. For 11:779

Nunez-Mir GC, Liebhold AM, Guo Q, Brockerhoff EG, Jo I, Ordonez K, Fei S (2017) Biotic resistance to exotic invasions: its role in forest ecosystems, confounding artifacts, and future directions. Biol Invasions 19:3287–3299

Paoletti E, Schaub M, Matyssek R, Wieser G, Augustaitis A, Bastrup-Birk AM et al (2010) Advances of air pollution science: From forest decline to multiple-stress effects on forest ecosystem services. Environ Pollut 158:1986–1989

Paquette A, Messier C (2010) The role of plantations in managing the world's forests in the Anthropocene. Front Ecol Environ 8:27–34

Parker, V. T., & Pickett, S. T. A. (1998). Historical contingency and multiple scales of dynamics within plant communities. In Ecological scale: theory and applications, Columbia University Press, pp. 171–192

Parks SA, Miller C, Parisien M-A, Holsinger LM, Dobrowski SZ, Abatzoglou J (2015) Wildland fire deficit and surplus in the western United States, 1984–2012. Ecosphere 6:1–13

Payn T, Carnus J-M, Freer-Smith P, Kimberley M, Kollert W, Liu S et al (2015) Changes in planted forests and future global implications. For Ecol Manage 352:57–67

Pohjanmies T, Triviño M, Tortorec EL, Mazziotta A, Snäll T, Mönkkönen M (2017) Impacts of forestry on boreal forests: An ecosystem services perspective. Ambio 46:743–755

Radeloff VC, Helmers DP, Kramer HA, Mockrin MH, Alexandre PM, Bar-Massada A et al (2018) Rapid growth of the US wildland-urban interface raises wildfire risk. Proc Natl Acad Sci 115:201718850

Raffa KF, Aukema B, Bentz BJ, Carroll A, Erbilgin N, Herms DA et al (2009) A Literal Use of 'Forest Health' Safeguards against Misuse and Misapplication. J Forest 107:276–277

Raffa KF, Aukema B, Bentz BJ, Carroll AL, Hicke JA., Kolb TE (2015) Responses of tree-killing bark beetles to a changing climate. In Climate change and insect pests. CABI, pp 173–201

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58:501–517

Raffa KF, Powell EN, Townsend PA (2013) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. Proc Natl Acad Sci USA 110:2193–2198

Reyer CPO, Brouwers N, Rammig A, Brook BW, Epila J, Grant RF et al (2015) Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J Ecol 103:5–15

Sambaraju KR, Carroll AL, Aukema BH (2019) Multiyear weather anomalies associated with range shifts by the mountain pine beetle preceding large epidemics. For Ecol Manage 438:86–95

Scheffer M (2009) Critical transitions in nature and society. Princeton University Press, Princeton, USA

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Seebens H, Bacher S, Blackburn TM, Capinha C, Dawson W, Dullinger S et al (2021) Projecting the continental accumulation of alien species through to 2050. Glob Change Biol 27:970–982

Seidl R, Müller J, Hothorn T, Bässler C, Heurich M, Kautz M (2016) Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. J Appl Ecol 53:530–540

Seidl R, Rammer W, Spies TA (2014) Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. Ecol Appl 24:2063–2077

Seidl R, Schelhaas M-J, Lexer MJ (2011) Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob Change Biol 17:2842–2852

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA (2016b) Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol 53:120–129

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G et al (2017) Forest disturbances under climate change. Nat Clim Chang 7:395–402

Showalter DN, Raffa KF, Sniezko RA, Herms DA, Liebhold AM, Smith JA, Bonello P (2018) Strategic development of tree resistance against forest pathogen and insect invasions in defense-free space. Front Ecol Evol 6:124

Shvidenko A, Barber CV, Persson R, Gonzales P, Hassan R, Lakyda P et al (2005). Forest and woodland systems. In M. de los Angeles & C. Sastry (eds) Millennium ecosystem assessment: current state & trends Aasessment. Island Press, Washington, pp 587–614

Sing L, Metzger MJ, Paterson JS, Ray D (2017) A review of the effects of forest management intensity on ecosystem services for northern European temperate forests with a focus on the UK. For: Int J For Res, 91:151–164.

Stadelmann G, Bugmann H, Wermelinger B, Bigler C (2014) Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. For Ecol Manage 318:167–174

Stephens SL, Collins BM, Fettig CJ, Finney MA, Hoffman CM, Knapp EE et al (2018) Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience 68:77–88

Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC et al (2018) Evidence for declining forest resilience to wildfires under climate change. Ecol Lett 21:243–252

Stireman JO, Dyer LA, Janzen DH, Singer MS, Lill JT, Marquis RJ et al (2005) Climatic unpredictability and parasitism of caterpillars: implications of global warming. Proc Natl Acad Sci USA 102:17384–17387

Strauss SY, Agrawal AA (1999) The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14:179–185

Straw NA, Williams DT, Kulinich O, Gninenko YI (2013) Distribution, impact and rate of spread of emerald ash borer Agrilus planipennis (Coleoptera: Buprestidae) in the Moscow region of Russia. For: Int J For Res, 86, 515–522.

Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. Ecol Appl 9:1189–1206

Taylor, S. W., & Carroll, A. L. (2004). Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. In: Shore TL , Brooks JE, Stone JE (eds) Mountain Pine Beetle Symposium: Challenges and Solutions . Natural Resources Canada, Canadian Forest Service, Victoria, BC, Canada, pp 41–51

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Thom D, Rammer W, Seidl R (2016) Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob Change Biol 23:269–282

Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biol Rev 91:760–781

Thompson ID, Guariguata MR, Okabe K, Bahamondez C, Nasi R, Heymell V, Sabogal C (2013) An operational framework for defining and monitoring forest degradation. Ecol Soc 18:1–23

Tkacz B, Moody B, Castillo JV, Fenn ME (2008) Forest health conditions in North America. Environ Pollut 155:409–425

Trumbore S, Brando P, Hartmann H (2015) Forest health and global change. Science 349:814–818

Turner MG (1989) Landscape Ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849

Turner MG, Baker WL, Peterson CJ, Peet RK (1998) Factors Influencing Succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523

Turner MG, Gardner RH (2015) Landscape ecology in theory and practice, pattern and process. 175–228.

Turner MG, Hargrove WW, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J Veg Sci 5:731–742

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of species diversity: recent revival of an old idea. Oikos 99:3–9

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S et al (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front Ecol Environ 8:135–144

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62:399–450

White PS, Pickett STA (1985) Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS (eds) The ecology of natural disturbance and patch dynamics. Academic Press, New York, NY, USA, pp 3–13

Whitman E, Parisien M-A, Thompson DK, Flannigan MD (2019) Short-interval wildfire and drought overwhelm boreal forest resilience. Sci Rep 9:18796

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:213–251

Williams AP, Abatzoglou JT, Gershunov A, Guzman-Morales J, Bishop DA, Balch JK, Lettenmaier DP (2019) Observed impacts of anthropogenic climate change on wildfire in California. Earth's Futur 7:892–910

Wingfield MJ, Brockerhoff EG, Wingfield BD, Slippers B (2015) Planted forest health: the need for a global strategy. Science 349:832–836

Woodall CW, Amacher MC, Bechtold WA, Coulston JW, Jovan S, Perry CH et al (2011) Status and future of the forest health indicators program of the USA. Environ Monit Assess 177:419–436

Young DJN, Stevens JT, Earles JM, Moore J, Ellis A, Jirka AL, Latimer AM (2017) Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol Lett 20:78–86

Zeng H, Peltola H, Väisänen H, Kellomäki S (2009) The effects of fragmentation on the susceptibility of a boreal forest ecosystem to wind damage. For Ecol Manage 257:1165–1173

Chapter 22
Climate Change and Forest Insect Pests

Andrea Battisti and Stig Larsson

22.1 Introduction

Climate change and the underlying causal factors have been thoroughly described (Field et al. 2014). Climate change, particularly increased temperature, has several consequences for the functioning of ecosystems. For instance, we know that the distribution range of some organisms has changed (Parmesan et al. 1999), tree phenology altered (Walther et al. 2002), and phenological asynchrony developed, e.g. between tree and associated insects (Visser and Both 2006). Although these effects are well understood and documented, we are only beginning to understand the effects of climate change on insect communities. This is in large part because of the complexity of their interactions with the abiotic and biotic environment.

It seems obvious that insect pest problems will be more important in a warmer climate because of the strong positive effect that temperature has on insect physiology and demography (Ayres and Lombardero 2000). However, temperature increases above optimal ranges may also be detrimental to insect fitness (Lehmann et al. 2020). In addition, it must be remembered that insect distribution and abundance are controlled by many factors other than temperature.

Klapwijk et al. (2012) reviewed climate-change associated factors affecting the outbreak potential of forest insects. They identified direct and indirect factors and provided a theoretical framework for assessing how changes in climate can be incorporated into predictive models of insect population dynamics. Similarly, Battisti and Larsson (2015) and Jactel et al. (2019) reviewed how climate change can affect the distribution range of insect pests, and provided examples of forest insect species whose ranges have been changed in a manner consistent with changes in climate.

A. Battisti (✉)
University of Padova, DAFNAE, Legnaro, Padova, Italy
e-mail: andrea.battisti@unipd.it

S. Larsson
Swedish University of Agricultural Sciences, Uppsala, Sweden

This chapter summarizes empirical evidence for climate-change induced insect pest problems, i.e. changed distribution range and frequency of insect outbreaks. Climate change can interact with non-native insect species accidently introduced into novel areas (Brockerhoff and Liebhold 2017). The issue of invasions is discussed in Chapter 23 of this volume. In this chapter we briefly discuss, in general terms, if and how climate change can be a factor that contributes to non-native insect species being established and becoming invasive, i.e. acting as novel pests in the forest.

Throughout the chapter the focus is on how climate change affects the distribution and abundance of forest pests (directly and indirectly through biotic interactions). We acknowledge that climate change will also influence host tree vulnerability and tolerance, and thus potential future damage (Toïgo et al. 2020; Forzieri et al. 2021) (discussed in Chapter 20).

22.2   Climatic Drivers

There is general consensus among scientists that the global climate is changing at an unprecedented rate, with many regions experience warming trends, shifts in precipitation patterns, and more frequent extreme weather events (Field et al. 2014). Factors potentially affecting forest insects include temperature, precipitation, rare weather events such as wind storms and heat waves, and atmospheric carbon dioxide concentration. All these factors can act both directly and indirectly (through host plant or natural enemies) on insect pests.

Temperature is the most important driver because it has steadily increased since the beginning of the twentieth century (0.61 °C in global mean temperature from 1850–1900 to 1986–2005; Field et al. 2014), and is predicted to increase further. Forests experience different levels of climate change depending on geographic position. Upper latitudes of northern and southern hemispheres, where most of the world's temperate and boreal forests grow, are expected to experience a higher warming. Insects, being poikilothermic organisms, respond directly to temperature as described by their specific reaction norms. Temperature also affects insects indirectly through effects on the host plant (bottom-up, see Chapter 7) and natural enemies (top-down, see Chapter 6).

Patterns in precipitation are due to a complex interaction between air circulation and temperature. Thus, an effect of temperature increase on precipitation patterns is expected. The result, however, is not as clear as the one depicted for temperature alone. Predictions on the total amount of annual precipitation vary according to the geographic area, with upper latitudes of both hemispheres experiencing more precipitation than mid latitudes, while the tropical and subtropical regions show a patchy effect (Field et al. 2014). Precipitation is also characterized by two more aspects, i.e. its distribution in the year and the intensity of the precipitation events. At upper latitudes of the northern hemisphere, precipitation increase will mainly occur in winter, while intense precipitation events will be more likely everywhere. Forests will thus experience different precipitation regimes according to geographic

region. The interactions of these changes with those of temperature and solar radiation (through modified cloudiness) will likely modify the microclimatic niche experienced by forest insects. Although precipitation is known to directly affect forest insects, most of its action is indirect because water availability is crucial for tree growth, and consequently, host quality for insect herbivores.

Extreme rare weather events, such as high/low temperature and rainfall, strong wind, and their combinations, will probably occur in higher frequency, and this is considered a potentially important component of climate change (Field et al. 2014). Two factors characterize the nature of these events, timing and intensity. For example, a heat wave may suppress all the insects active in that moment because the upper thermal threshold is achieved (see Chapter 4), or a wind storm may simultaneously fell a large number of trees that may facilitate a bark beetle outbreak (see Chapter 10). The periods when such events may happen are roughly predictable, because they are associated with the yearly variation of both temperature and precipitation, although it is impossible to define exactly when and where they will occur.

Carbon dioxide, together with other greenhouse gases, is a major determinant of temperature increase (Field et al. 2014). Being a fundamental molecule for photosynthesis, the increase in carbon dioxide in the atmosphere may affect the metabolism of forest trees, including molecules of importance to tree-feeding insects (Lindroth et al. 1993), although the general effects on herbivorous insects are weak and idiosyncratic (Hillstrom et al. 2014).

The climate in the future will most likely differ in all the above-mentioned aspects. However, with respect to effects on forest insects temperature has by far been the most discussed in the literature, and thus is the factor for which there exists a reasonable amount of data. Therefore, it will be the focus of discussion in the following sections.

22.3   Insect Response to Increased Temperature

In this section we deal with temperature effects at the level of the individual insect. Temperature has a direct effect on insect development rate and survival. Development rate generally increases with increasing temperature to some maximum, above which development slows down and mortality increases (see Chapter 4). Increased development rate could lead to increased voltinism in facultative multivoltine species. Increased development rate in insect larvae could result in reduced temporal exposure to enemies or other mortality agents, with resulting higher survival.

Winter mortality is likely to decrease under increasing temperatures (e.g. Ayres and Lombardero 2000), although decreased snow cover (and therefore decreased insulation of overwintering sites) can reverse that pattern (Petrucco-Toffolo and Battisti 2008). Warmer winters may permit some non–diapausing species to continue feeding and development during months that were previously too cold (Schneider et al. 2021). For example, larvae of the pine processionary moth *Thaumetopoea pityocampa* have a higher probability of survival if winter temperatures do not often fall below specific feeding thresholds (Battisti et al. 2005, Fig. 22.1A, B).
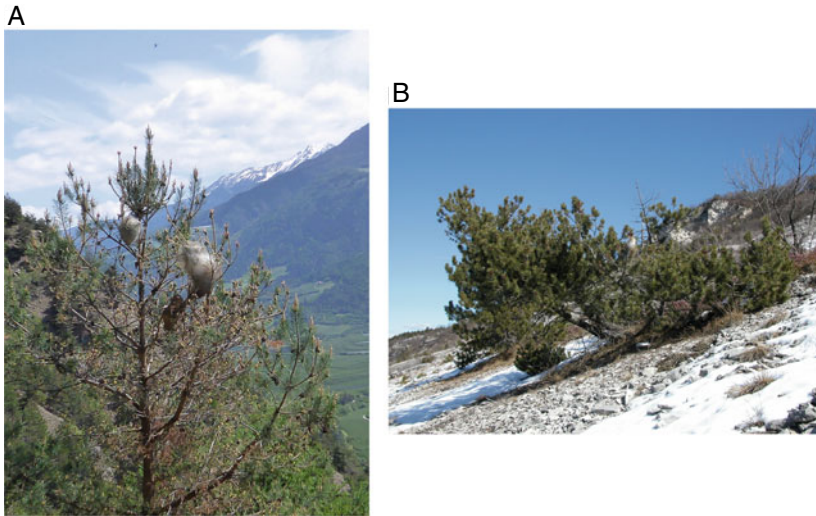
Fig. 22.1 **A** The same tree can be colonized in subsequent years as shown in the photo where the remains of an old nest are visible close to two new nests with white silk. The tree is a Scots pine (*Pinus sylvestris*) growing at high elevation (>1,400 m) in the Southern Alps (Venosta/Vinschgau valley) where the insect has expanded its distribution in recent decades and reached the upper limit of host plant range. At even higher elevations in the Alps, the pine processionary moth is massively colonizing the dwarf mountain pine (*Pinus mugo*), historically not a suitable host because of being covered by snow. **B** The photo shows a colony that survived the winter because the limited snow cover, and higher temperatures, permitted suitable conditions for larval feeding across the winter.

Several indirect effects mediated through the host tree exist. Many insect species match their feeding activity with certain developmental stages in the host plant; for example, species associated with deciduous trees, such as the autumnal moth *Epirrita autumnata*, match their feeding with nutritious immature foliage during spring and early summer (Haukioja 2003).

If host trees are reasonably well matched to historically favorable climatic conditions, then it is inevitable that changing climate will lead to situations where trees are poorly matched to the new conditions, i.e. trees can be stressed. Stress-induced changes in plant tissue quality and their effects on insect survival and reproduction are well documented in experimental studies (Koricheva et al. 1998).

That plant stress can trigger insect outbreaks is a long-standing hypothesis in forest entomology. Insect outbreaks have been commonly correlated with conditions that induce stress in their host plants (e.g. Mattson and Haack 1987). This has led to speculation that there is a causal link between stress-induced changes in plant quality, and thus insect performance, and the start of outbreaks (e.g. White 1974). Experimental tests of the plant stress hypothesis, most often at the level of individual insects, have produced mixed results; species from some feeding guilds respond to experimentally stressed trees with increased performance, some are unaffected, and some respond negatively (Larsson 1989). Bark beetles constitute a globally important

group of insects for which plant stress seems relevant; a long-standing paradigm is that healthy trees are resistant to most bark beetle species (and other boring insects), but that periods of stress make trees susceptible, although at high beetle density even non-stressed trees can be attacked and killed (Raffa et al. 2008).

Arthropod natural enemies can exert powerful forces on the performance of herbivorous insects (see Chapter 6), and climate change may affect their activity as much as that of their prey. In addition, the phenological synchrony between natural enemies and their hosts/prey can also be affected. However, specialist enemies should be under strong selection to track phenological changes in their prey, which might make them less likely to become temporally uncoupled from their prey (Klapwijk et al. 2010). Higher temperatures can influence parasitism and predation rates by increasing searching activity of individual parasitoids and predators. When the prey are relatively immobile (e.g. many immature insect herbivores), this should generally increase rates of detection and attack.

Insect pathogens, e.g. fungi, bacteria, and viruses, can also limit the performance of herbivorous insects (Hajek 1997). Temperature can be important for both infection rate and defense responses within the host. Different thermal optima for host and pathogen might lead to a situation where high temperatures favor the host by both optimizing defense responses and directly limiting pathogen growth (Blanford and Thomas 1999).

Insects rarely, if ever, act independently from other organisms. Therefore, it is necessary to consider the position of the forest insect in the trophic web. In other words, not only should we consider direct effects of climate change on the target insect, but we need to recognize likely interactions of climatic variables with host tree, natural enemies, and insect diseases (indirect effects). Such an approach is necessary to fully understand the potential consequences that climate change can have for pests. For climate-change driven effects to have an impact on forest ecosystems, and thus be of economic concern for forest managers, effects at the level of individual insects need to be confirmed at the level of the population. This is not a trivial step as a multitude of biotic interactions, each with its inherent uncertainty, can modify the effects when it comes to populations, as discussed in the following section.

22.4 Insect Population Response to Increased Temperature

Climate warming can influence two important aspects of insect population ecology: distribution and abundance. Many insect species have been documented to change their distribution range in response to increased temperature (Battisti and Larsson 2015). It is important to realize, however, that the dynamics of range expansion are rarely known in any detail. This is simply because populations in expansion areas are initially at very low density and thus can remain undetected for a long time. If the expanding population is a forest pest, then the expansion is likely to be discovered if the population reaches outbreak numbers.

In general, the majority of insect populations are controlled by a number of different agents and thus occur at low density. Under some conditions an insect species may escape from the controlling agents and reach outbreak densities. Outbreaks are easily observed because they are generally defined by managers as population densities so high that they are of economic concern in forestry. Outbreaks can thus be seen as a proxy for high-density events, and of course as a warning signal of potential forest health problems. Low-density populations will also vary in size, but their dynamics will most of the time be unnoticed because their densities will not result in damage to the forest.

In the following section, we present case studies to illustrate effects of climate change on insect populations. The focus is on outbreaks, which we assign to three main groups. The first group of case studies refer to *Outbreaks at the core of historical range of distribution,* thus evidence of climate change effects (or lack of effects) on populations in the historic range of the distribution. The second group deals with *New areas of outbreaks within historic species distribution.* This refers to species where no outbreaks were recorded for a portion of their historical distribution, typically in the colder areas, but where outbreaks in recent years have been observed. The third group includes *Outbreaks in recently invaded geographic areas,* in other words, species that have expanded their distribution range and occurred at outbreak densities that clearly can be related to warming.

22.4.1 Outbreaks at the Core of Historical Range of Distribution

Long-term surveillance data of European insect populations report a large variability in the responses of key forest pests to climate change: positive, negative, and no response to increased temperatures (Haynes et al. 2014; Lehmann et al. 2020).

The European spruce beetle *Ips typographus* is the most aggressive bark beetle in Europe. Analysis of 17 time-series spanning from 1980 to 2010 shows density-dependent factors to be the main drivers of population dynamics, although high temperature and summer precipitation deficit also play a role (Marini et al. 2017). In addition, temperature appears to be important for the voltinism of *I. typographus*, as populations may become bi- or multivoltine under favorable conditions (Wermelinger 2004). Results suggest that greater efforts should be made to integrate temperature increase, drought, and storm effects into future scenarios of outbreaks under climate change (Marini et al. 2017).

The larch bud moth *Zeiraphera griseana* is an example of a pest where climate warming has had negative effects on population growth. Dendrochronological analyses of host trees associated with *Z. griseana* outbreaks over 500 years reveal periodicities of 4, 8, and 16 years throughout the time series, except during the period 1690–1790, and since 1980. The data suggest a disruption of periodicity probably

related to changes in climate; temperature decreased in the period 1690–1790 (Little Ice Age) wheras it increased since 1980 (Saulnier et al. 2017).

Responses at the species level appear idiosyncratic and no general patterns were observed in several species of defoliating insects associated with coniferous trees in southern Germany for more than 200 years (Haynes et al. 2014). A similar study in Hungary involving five species of defoliating insects associated with broadleaved tree species for a period of about 60 years also observed no clear pattern in responses (Klapwijk et al. 2013). It should be noted that for both these studies data refer to large scale events, and that changes at local scale could have gone undetected. More precise data are available for the pine processionary moth *Thaumetopoea pityocampa* from eight geographic zones in France (but for a shorter period, 1981–2014). Although in general, populations were controlled mainly by density-dependent agents, population growth was negatively related to precipitation in five regions and positively related to winter temperature in four regions; thus, these data suggest that the effects of weather-related factors need to be considered at a local scale using appropriate measures of population density (Toïgo et al. 2017).

22.4.2 New Areas of Outbreaks Within Historic Species Distribution

Both the autumnal moth *Epirrita autumnata* and the winter moth *Operophtera brumata* have expanded their outbreak range in recent years, presumably as a result of improved winter survival of eggs, and maintenance of synchrony (through adaptive phenological plasticity) with bud burst of their main host, the mountain birch *Betula pubescens* ssp. *tortuosa* (Jepsen et al. 2008). Winter moth populations show a pronounced north-eastern expansion of outbreaks into areas previously dominated by the autumnal moth, which in turn has expanded historically into colder areas (Tenow 1996). This has been possible because eggs of the autumnal moth are more cold tolerant than those of the winter moth. This important direct effect of increased temperature can be affected by indirect effects in the trophic interactions and in the synchronization with the bud break of the host plants. In subarctic mountain birch forests, predation rates on *E. autumnata* and *O. brumata* larvae were almost twice as high in low versus high elevation sites, indicating that release from predation pressure at high elevations can favor outbreaks in these cooler habitats (Pepi et al. 2017).

Records of spruce budworm (*Choristoneura fumiferana*) defoliation and tree-ring analysis indicate that the outbreak range of this insect has expanded to the north. A regional tree-ring chronology performed by Boulanger et al. (2012) represents the longest and most replicated reconstruction of outbreak dynamics in North America (1551–1995). The authors identified nine potential outbreaks and three uncertain outbreaks in a 400-year period and concluded that outbreak frequency varied with temperature, being less frequent during the 1660–1850 period (every ~ 50 years,

Little Ice Age) and more frequent in warmer periods like prior to 1660 (every ~ 28 years) and during the twentieth century (every ~ 30 years). The simultaneous occurrence of a general increase in temperature in northern latitudes at the start of the last outbreak indicates a relation with climate change (Candau and Fleming 2011). An interesting indirect effect involving the host plant has been suggested. The main host of the spruce budworm is balsam fir *Abies balsamea*, whereas black spruce *Picea mariana* is a secondary host. Climate change is predicted to advance the phenology of the secondary host that is more abundant at the upper latitudinal edge, making it more susceptible to defoliation, and thus facilitating expansion of the outbreak area into higher latitudes (Pureswaran et al. 2015). This factor has been hypothesized to explain the occurrence of the new outbreak that started in 2006 about four degrees (445 km) of latitude north of the previous one (1966–1992), with a prediction for a more northern expansion in 2041–2070 (Régnière et al. 2012).

In the southern hemisphere, the defoliation of *Nothofagus* forests by the saturnid moths of the genus *Ormiscodes* have been associated with drier and warmer seasons. The outbreaks have been more frequent in southern than in northern Patagonia. Results are consistent with recent warming in southern Patagonia and suggest that outbreak frequency may continue to increase with further warming (Paritsis and Veblen 2011).

22.4.3   Outbreaks in Recently Invaded Geographic Areas

In recent decades, the pine processionary moth *T. pityocampa* has expanded its latitudinal and elevational distribution range (Battisti et al. 2005). Improved survival during the feeding period in winter has contributed to outbreaks in pine forests previously unoccupied in France, Italy, Spain, and Turkey. Rapid range expansion is facilitated by warm summer nights that contribute to long-distance (more than 2 km) dispersal of female moths (Battisti et al. 2006). In the newly occupied areas, however, population dynamics are driven more by density-dependent agents than by climatic drivers (Tamburini et al. 2013). Thus, once the expansion area is occupied population dynamics seem to be determined by the same factors as in the historical range, provided that specialist enemies have tracked the host in the new areas. Interestingly, *T. pityocampa* shows prolonged diapause facilitating persistence in the newly colonized areas even if the weather turns unfavorable for one or more years; diapause can last up to eight years with some individuals emerging every year (Salman et al. 2016).

In western Canada recent outbreaks of the mountain pine beetle *Dendroctonus ponderosae* have led to extensive tree mortality within at least 14 million hectares of lodgepole pine *Pinus contorta* forests. The start of the outbreak was facilitated by fire suppression during the last century, which created large tracts of over-mature pine stands, in combination with recent climatic patterns, viz. mild winters and warm dry summers (Raffa et al. 2008; Bentz and Jönsson 2015). However, the relative

importance of large areas of susceptible pine forests and suitable climatic conditions for beetle population growth is not entirely clear (Cooke and Carroll 2017).

In general, bark beetle species associated with weakened trees are difficult to detect at low-densities, whereas damage and tree mortality become obvious during outbreaks. Therefore, the range edge generally considered is that of the epidemic range, whereas the margins of the endemic range remain largely unknown. In south-east USA, the distribution of the southern pine beetle *Dendroctonus frontalis* has been moved northwards due to milder winters that enhance beetle performance (Ungerer et al. 1999). Similarly, spruce bark beetle (*Dendroctonus rufipennis*) outbreaks may occur throughout the range of spruce in North America in the future. In its coldest locations, *D. rufipennis* is semivoltine, having a generation every two years and outbreaks are rare in these populations (Schebeck et al., 2017).

22.5   Invasive Species and Climate Change

The increasing problem with invasive species during the last decades may be linked to climate change although the evidence for this remain limited. Global trade and travel are the major drivers of the invasion process (Ramsfield et al. 2016; Brockerhoff and Liebhold 2017). The process of invasion is often divided into several phases (pre-transport, transport, arrival, establishment, and spread; see Chapter 23). Here we briefly discuss how changes in climate can interact with trade and travel in each of the invasion phases.

Very little can be said about the pre-establishment phases (pre-transport, transport, arrival). It is obvious that propagule pressure in the area of origin is important in order to assess the probability of transportation, but it is unclear to what extent changes in climate affect propagule pressure. The next two phases (establishment and spread) are clearly linked to climate change as they depend on the matching between the area of origin and the area of arrival. The impact of climate change on climate matching between areas of origin and destination on the establishment and spread of non-native species is difficult to assess as data about failure to establish are rarely available for forest insects. The increasing number of the incursions of ambrosia beetles from tropical and subtropical regions in temperate forests could be an example of how this category of organisms is favored by climate change (Rassati et al. 2016). The inclusion of climatic responses of pests in the risk assessment of invasive species may help to predict which ones are the most likely to get established and threat newly colonized habitats (Grousset et al. 2020).

The spread of invasive species in a newly colonized area depend on niche availability and dispersal traits of the insect, and in principle does not differ from that of native species (Pureswaran et al. 2018). The hemlock woolly adelgid *Adelges tsugae* was introduced into Virgina, eastern USA in the mid 1900s. Increase in mean minimum winter temperature resulted in higher survival in overwintering life stages and facilitated the expansion northwards in the eastern USA (Paradis et al. 2008). The build up of high density populations in the already colonized areas contributed

greatly to hemlock (*Tsuga canadensis*, *T. caroliniana*) dieback (Fitzpatrick et al. 2012).

Once established, the response of invasive species to climatic factors may be similar to that of native species, as illustrated by the spongy moth *Lymantria dispar*. The population dynamics of *L. dispar* have been thoroughly documented in the USA, showing periods of cyclic outbreaks intermingled by periods with no cycles. The dynamics seem to be driven by trophic interactions while the role of climate appears to be negligible (Allstadt et al. 2013). It is not clear if a changing climate would cause a net increase in suitable habitat for invading insects such as spongy moth in North America, as there should be some areas that become more favorable and others that become less favorable (Tobin et al. 2014).

22.6 Conclusions

Climate change, in particular increased temperature, is certain to have qualitative and quantitative effects on insect populations, primarily because temperature ultimately sets the limit for most insect distribution ranges (Battisti and Larsson 2015). For insects on trees, however, the availability of the host tree(s) will be a critical factor because most insect species are associated with one or a few host tree species only. The expected slower range expansion by trees compared with that of the insects, because of the much longer generation time of trees, will likely slow down the successful expansion of the insects. Overall, this probably means that at a certain point in time host tree availability, rather than temperature, may set the limit for future insect range expansion. This scenario would only apply to insect species not able to switch to novel host tree species in the expansion area.

Climate-change attention is mostly on insect species expanding their range into geographic areas that have become climatically more favorable. We have to assume, however, that an equally large area may become unfavorable. In contrast to expansion, such retraction of the range at the lower edge of the distribution will not be as immediate as the expansion, mainly because plants do not react as quickly to the warming as insects do. This is why a net increase in areal distribution is expected in the short-term while in a medium-long term a general shift of the range is predicted.

A difficult task is to assess whether or not damage to forests will be more, or less, severe under climate change (Jactel et al. 2019; Lehmann et al. 2020). The degree of damage is usually positively related to the density of the insect pest population. Thus, we can reformulate the issue using outbreak as a proxy for damage and ask: are outbreaks likely to be more common under climate change?

Ideally, in order to scientifically analyze this issue we should be able to refer to the frequency of outbreaks for a scenario of no climate warming. Obviously, this is not a straightforward matter, but the literature provides important information about insect populations that can be used as a simple null model of outbreak frequency (Barbosa and Schultz 1987). Most insect populations in forest ecosystems thrive around low mean densities, far below outbreak densities (Landsberg and Ohmart 1989), meaning

that they are efficiently controlled by several, mostly unknown factors. It also indicates that many insect populations often remain unnoticed for a long time (endemic) and are considered pests only when they build up epidemic populations (outbreak) (Barbosa et al. 2012).

The categorization of forest insect populations outlined above is simplistic, but still useful as a basis for the following discussion of forest damage and insect pests under future climate change. We envisage four situations:

1. The extent of range expansion of non-outbreak insects is virtually unknown; this should come as no surprise because, by definition, these insect species occur at low density. It is quite likely, however, that such expansion has occurred but should be of minor importance from a management point of view, given that the population ecology of these putative species in the new area is similar to that in their core area.
2. A bias exists in the literature with almost all evidence of climate-change effects coming from outbreak species, for obvious reasons (easy to observe). In the event that outbreaks occur in the expanded range, an important question will then be whether the outbreak dynamics are similar to those in the original distribution range or show new characteristics (the mountain pine beetle outbreak may be an example of this as it has invaded new host tree species, such as *Pinus banksiana* in Alberta, creating the potential for massive range expansion into north central and eastern north America).
3. Outbreaks in the historical area can be more, or less, frequent under climate change depending on the life history of the insect and how climate affects biotic interactions (with host tree, natural enemies, insect pathogens). Forest management is changing in many parts of the world, e.g. with stands being overall more intensively managed than in the past. So far, there are no data to suggest that pest dynamics are significantly different under intensive forestry, such as nitrogen fertilization of natural stands (Kytö et al. 1996). If novel management practices, e.g. for maximizing carbon sequestration, will be introduced on a large scale, then there is certainly a risk that pest problems will follow.
4. Forest health problems due to non-native insect species will most likely continue to increase in the future. Some non-natives will establish but with dynamics of the low-density type. The distribution of other non-natives will expand, perhaps as a consequence of climate change, and establish in natural forests where populations increase to outbreak level (thus becoming an invasive). An especially serious threat is the situation where non-native insects establish in plantations of non-native tree species. Here managers may be faced with a situation of intensive control practice most often not necessary in traditional forestry, such as the application of biological control with a parasitic nematode against the *Sirex* wood wasp in pine plantations (Slippers et al. 2015).

The science of outbreak dynamics includes data from economically important insect populations whose dynamics appear to be driven by factors that differ from those of non-outbreak species (e.g. Larsson et al. 1993). Thus, there is no overarching hypothesis based on logic (or data) that allows for specific predictions at the species

(or population) level. Our approach has been to use information from the past in order to understand the future. This approach allows us to take advantage of existing scientific knowledge. Although we advocate this approach we emphasize that we also need to appreciate that the available data, and thus predictions based on these data, have a substantial degree of uncertainty. Very rarely, if ever, can outbreak data be considered replicated, due to different boundary conditions. This is a situation that is true for many ecological data sets meant to be used in policy, but is especially troublesome here because we are interested in changes over long periods of time, hundreds of years.

References

Allstadt AJ, Haynes KJ, Liebhold AM, Johnson DM (2013) Long-term shifts in the cyclicity of outbreaks of a forest-defoliating insect. Oecologia 172:141–151

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286

Barbosa P, Schultz JC (1987) Insect outbreaks. Academic Press, New York

Barbosa P, Letourneau DK, Agrawal AA (2012) Insect outbreaks revisited. Academic Press, New York

Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol Appl 15:2084–2096

Battisti A, & Larsson S (2015) Climate change and insect pest distribution range. In C. Björkman & P. Niemelä, editors. Climate change and insect pests. CABI International, pp 1–15

Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. Glob Change Biol 12:662–671

Bentz BJ, Jönsson AM (2015) Modeling bark beetle responses to climate change. In: Vega FE, Hofstetter RW (eds) Bark Beetles. Academic Press, San Diego, pp 533–553

Blanford S, Thomas MB (1999) Host thermal biology: the key to understanding host–pathogen interactions and microbial pest control? Agric for Entomol 1:195–202

Boulanger Y, Arseneault D, Morin H, Jardon Y, Bertrand P, Dagneau C (2012) Dendrochronological reconstruction of spruce budworm (*Choristoneura fumiferana*) outbreaks in southern Quebec for the last 400 years. Can J For Res 42:1264–1276

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biol Invasions 19:3141–3159

Candau J-N, Fleming R (2011) Forecasting the response of spruce budworm defoliation to climate change in Ontario. Can J For Res 41:1948–1960

Cooke BJ, Carroll AL (2017) Predicting the risk of mountain pine beetle spread to eastern pine forests: considering uncertainty in uncertain times. For Ecol Manage 396:11–25

Field CB, Barros VR, Mach KJ et al. (2014). Climate change 2014: impacts, adaptation, and vulnerability. part A: global and sectoral aspects. Contribution of Working Group II to the fifth

assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 35–94

Fitzpatrick MC, Preisser EL, Porter A, Elkinton J, Ellison AM (2012) Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. Ecol Appl 22:472–486

Forzieri G, Girardello M, Ceccherini G, Spinoni J, Feyen L, Hartmann H, Beck PSA, Camps-Valls G, Chirici G, Mauri A, Cescatti A (2021) Emergent vulnerability to climate-driven disturbances in European forests. Nat Commun 12:1081

Grousset F, Grégoire J-C, Jactel H, Battisti A, Benko Beloglavec A, Hrašovec B, Hulcr J, Inward D, Orlinski A, Petter F (2020) The risk of bark and ambrosia beetles associated with imported non-coniferous wood and potential horizontal phytosanitary measures. Forests 11:342

Hajek AE (1997) Ecology of terrestrial fungal entomopathogens. Adv Microb Ecol 15:193–249

Haukioja E (2003) Putting the insect into the birch–insect interaction. Oecologia 136:161–168

Haynes KJ, Allstadt AJ, Klimetzek D (2014) Forest defoliator outbreaks under climate change: Effects on the frequency and severity of outbreaks of five pine insect pests. Glob Change Biol 20:2004–2018

Hillstrom ML, Couture JJ, Lindroth RL (2014) Elevated carbon dioxide and ozone have weak, idiosyncratic effects on herbivorous forest insect abundance, species richness, and community composition. Insect Conservation and Diversity 7:553–562

Jactel H, Koricheva J, Castagneyrol B (2019) Responses of forest insect pests to climate change: not so simple. Current opinion in Insect Science 35:103–108

Jepsen JU, Hagen SB, Ims RA, Yoccoz NG (2008) Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. J Anim Ecol 77:257–264

Klapwijk MJ, Grobler BC, Ward K, Wheeler D, Lewis OT (2010) Influence of experimental warming and shading on host–parasitoid synchrony. Glob Change Biol 16:102–112

Klapwijk MJ, Ayres MP, Battisti A, Larsson S (2012) Assessing the impact of climate change on outbreak potential. In: Barbosa P, Letourneau DK, Agrawal AA (eds) Insect outbreaks revisited. Academic Press, New York, pp 429–450

Klapwijk MJ, Csóka G, Hirka A, Björkman C (2013) Forest insects and climate change: long-term trends in herbivore damage. Ecol Evol 3:4183–4196

Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. Annu Rev Entomol 43:195–216

Kytö M, Niemelä P, Larsson S (1996) Insects on trees: population and individual response to fertilization. Oikos 75:148–159

Landsberg J, Ohmart C (1989) Levels of insect defoliation in forests: patterns and concepts. Trends Ecol Evol 4:96–100

Larsson S (1989) Stressful times for the plant stress—insect performance hypothesis. Oikos 56:277–283

Larsson S, Björkman C, Kidd NAC (1993) Outbreaks in diprionid sawflies: why some species and not others? In: Wagner MR, Raffa KF (eds) Sawfly life history adaptations to woody plants. Academic Press, San Diego, pp 453–483

Lehmann P, Ammunét T, Barton M, Battisti A, Eigenbrode SD, Jepsen JU, Kalinkat G, Neuvonen S, Niemelä P, Terblanche JS, Økland B, Björkman C (2020) Complex responses of global insect pests to climate warming. Front Ecol Environ 18:141–150

Lindroth RL, Kinney KK, Platz CL (1993) Responses of deciduous trees to elevated atmospheric CO_2: productivity, phytochemistry, and insect performance. Ecology 74:763–777

Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, Grégoire J-C, Hurling R, Nageleisen LM, Netherer S, Ravn HP, Weed A, Schroeder M (2017) Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography 40:1426–1435

Mattson WJ, Haack RA (1987) The role of drought stress in provoking outbreaks of phytophagous insects. In: Barbosa P, Schultz JC (eds) Insect Outbreaks. Academic Press, San Diego, pp 365–394

Paradis A, Elkinton J, Hayhoe K, Buonaccorsi J (2008) Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitig Adapt Strat Glob Change 13:541–554

Paritsis J, Veblen TT (2011) Dendroecological analysis of defoliator outbreaks on *Nothofagus pumilio* and their relation to climate variability in the Patagonian Andes. Glob Change Biol 17:239–253

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583

Pepi AA, Vinstad OPL, Ek M, Jepsen JU (2017) Elevationally biased avian predation as a contributor to the spatial distribution of geometrid moth outbreaks in sub-arctic mountain birch forest. Ecological Entomology 42:430–438

Petrucco-Toffolo E, Battisti A (2008) Performances of an expanding insect under elevated CO_2 and snow cover in the Alps. Iforest Biogeosciences For 1:126–131

Pureswaran DS, De Grandpré LD, Paré D, Taylor A, Barrette M, Morin H, Régnière J, Kneeshaw DD (2015) Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forests. Ecology 96:1480–1491

Pureswaran DS, Roques A, Battisti A (2018) Forest insects and climate change. Curr For Rep 4:35–50

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58:501–517

Ramsfield TD, Bentz BJ, Faccoli M, Jactel H, Brockerhoff EG (2016) Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts. Forestry 89:245–252

Rassati D, Faccoli M, Haack RA, Battisti A, Marini L (2016) Bark and ambrosia beetles show different invasion patterns in the USA. PLoS One 11(7):e0158519

Régnière J, St-Amant R, Duval P (2012) Predicting insect distributions under climate change from physiological responses: spruce budworm as an example. Biol Invasions 14:1571–1586

Salman HR, Hellrigl K, Minerbi S, Battisti A (2016) Prolonged pupal diapause drives population dynamics of the pine processionary moth (*Thaumetopoea pityocampa*) in an outbreak expansion area. For Ecol Manage 361:375–381

Saulnier M, Roques A, Guibal F, Rozenberg P, Saracco G, Corona C, Edouard J-L (2017) Spatiotemporal heterogeneity of larch budmoth outbreaks in the French Alps over the last 500 years. Can J For Res 47:667–680

Schebeck M, Hansen E, Schopf A, Gregory R, Stauffer C, Bentz B (2017) Diapause and overwintering of two spruce bark beetle species. Physiol Entomol 42:200–210

Schneider L, Comte V, Rebetez M (2021) Increasingly favourable winter temperature conditions for major crop and forest insect pest species in Switzerland. Agric for Meteorol 298–299:108315

Slippers B, Hurley BP, Wingfield MJ (2015) Sirex woodwasp: A model for evolving management paradigms of invasive forest pests. Annu Rev Entomol 60:601–619

Tamburini G, Marini L, Hellrigl K, Salvadori C, Battisti A (2013) Effects of climate and density-dependent factors on population dynamics of the pine processionary moth in the Southern Alps. Clim Change 121:701–712

Tenow O (1996) Hazards to a mountain birch forest—Abisko in perspective. Ecol Bull 45:104–114

Tobin PC, Gray DR, Liebhold AM (2014) Supraoptimal temperatures influence the range dynamics of a non-native insect. Divers Distrib 20:813–823

Toïgo M, Barraquand F, Barnagaud J-Y, Piou D, Jactel H (2017) Geographical variation in climatic drivers of the pine processionary moth population dynamics. For Ecol Manage 404:141–155

Toïgo M, Nicolas M, Jonard M, Croisé L, Nageleisen LM, Jactel H (2020) Temporal trends in tree defoliation and response to multiple biotic and abiotic stresses. For Ecol Manage 477:118476

Ungerer MJ, Ayres MP, Lombardero MJ (1999) Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). J Biogeogr 26:1133–1145

Visser ME, Both C (2006) Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the royal society of London series B—Biol Sci 272:2561–2569

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395

Wermelinger B (2004) Ecology and management of the spruce bark beetle, *Ips typographus*—a review of recent research. For Ecol Manage 202:67–82

White TCR (1974) Hypothesis to explain outbreaks of looper caterpillars, with special reference to population of *Selidosema suavis* in a plantation of *Pinus radiata* in New-Zealand. Oecologia 16:279–301