ANNUAL REVIEWS

Annual Review of Entomology

Impact of Stand and Landscape Management on Forest Pest Damage

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Annu. Rev. Entomol. 2022. 67:181–99

The *Annual Review of Entomology* is online at ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-062321-065511

Keywords

diversity, forestry, heterogeneity, landscape, outbreak, pest

Abstract

One promising approach to mitigate the negative impacts of insect pests in forests is to adapt forestry practices to create ecosystems that are more resistant and resilient to biotic disturbances. At the stand scale, local stand management practices often cause idiosyncratic effects on forest pests depending on the environmental context and the focal pest species. However, increasing tree diversity appears to be a general strategy for reducing pest damage across several forest types. At the landscape scale, increasing forest heterogeneity (e.g., intermixing different forest types and/or age classes) represents a promising frontier for improving forest resistance and resilience and for avoiding large-scale outbreaks. In addition to their greater resilience, heterogeneous forest landscapes frequently support a wide range of ecosystem functions and services. A challenge will be to develop cooperation and coordination among multiple actors at spatial scales that transcend historical practices in forest management.

1. INTRODUCTION

Landscape: a habitat mosaic of interacting patches that can be visited by the organisms under consideration

Short-rotation forestry: growing trees in extremely dense stands harvested at 3–4-year intervals, mostly for biofuel production

Forest ecosystems have never been so threatened by insect pests (72, 145), which can cause important economic losses and negative impacts on biodiversity and ecosystem functioning (18). These growing risks are linked to multiple global change pressures, i.e., climate and land-use changes and increased invasions by non-native species (7). Warmer and drier conditions and more frequent extreme events (e.g., storms and wildfires) are triggering severe and widespread insect outbreaks because insects, which are poikilothermic organisms, can develop faster, expand their range, and benefit from the increasing availability of less defended trees (90, 91, 130). At the same time, the number of insect management options has decreased significantly. In most countries, insecticides are banned due to their inefficiency and growing concerns about their impacts on the environment (82), and the promises of tree genetic selection for insect resistance have not yet been fulfilled (56, 151, 152). Thus, there is an urgent need to develop effective and more environmentally friendly methods to protect our forests. One promising approach is to tailor forest management to promote forest stands and landscapes that are more resistant and resilient to insect disturbances.

First, by shaping local species composition and the structure of tree communities, forest management can have important consequences for host quality; tree defenses; and multitrophic interactions involving host trees, pests, and their natural enemies (68, 75). Second, at larger spatial scales, forest management also shapes the structure of landscapes, affecting the composition and configuration of the habitat mosaics by changing the size and type of forest stands that constitute them, with potential effects on pest dispersal and regional population dynamics (150). Third, after insect outbreaks have occurred, entomologists and foresters are often asked to implement emergency measures to reduce the negative ecological and economic consequences of these disturbances on standing forests. Although there is a long history of such interventions, mostly across temperate ecosystems, there is still very little consensus on best practices due to the lack of scientific assessment of outcomes from different strategies (31).

We focus on three specific aims: (*a*) to evaluate the effect of forest management at the stand scale on the resistance to insect herbivory, (*b*) to scale up predictions of forest management effects on insect populations from the stand to the landscape and regional scales, and (*c*) to evaluate the efficacy of reactive forest management practices in containing or suppressing ongoing outbreaks. On the one hand, in several temperate or boreal countries, there is a long history of sustainable forest management that has developed a wide array of management practices providing a portfolio of options to modify forest resistance to insect herbivory. On the other hand, the documentation of outbreaks in the tropics remains scant (37), and it was not possible to find studies evaluating the role of forest management on insect outbreaks in these regions. Due to the disproportionate body of research in temperate forests, and secondarily in boreal forests, this review focuses on these biomes. In addition, this review mostly focuses on managed forests, from intensive productive stands to multifunctional semi-natural forests, and it does not cover very simplified systems such as short-rotation forestry for biomass production. Due to the lack of studies, it was also impossible to evaluate the cost effectiveness of the implementation of the different management strategies.

2. EFFECT OF FOREST MANAGEMENT AT THE STAND SCALE

In this section, we synthesize the effects of local management practices at the stand scale on forest resistance to insect damage. We define a forest stand as an operational management unit made up of a contiguous community of trees homogeneous in terms of management and sufficiently uniform in composition and structure to be distinguished from adjacent communities. The spatial scale of stands defined in this way tends to be thousands of square meters to dozens of hectares,

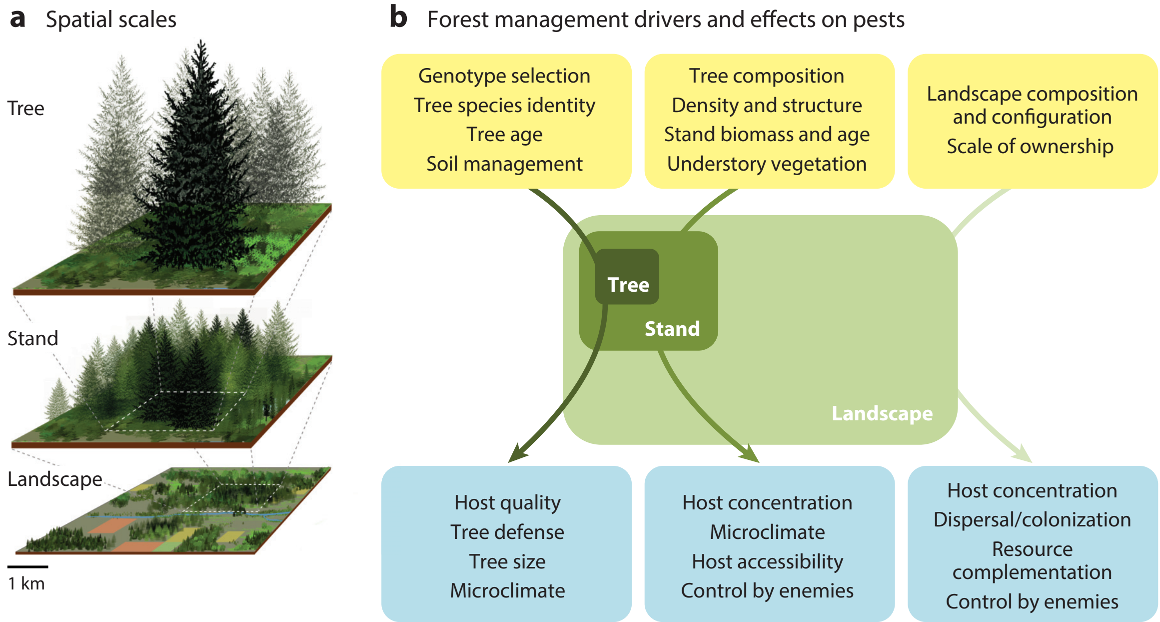

Figure 1

Multiscale effects of forest management on pest insects. (*a*) Forest management affects pests at multiple spatial scales, from tree-level to landscape-level processes. (*b*) Local stand management modifies both local tree conditions and landscape patterns, affecting multitrophic interactions among plants, herbivores, and natural enemies.

but with regional variation (e.g., larger stands in North America than in Western Europe) (**Figure 1**).

2.1. Shaping Forest Composition

Managed forests can greatly vary in their tree composition, from monospecific to highly diverse communities depending on climate, forest type, and forestry aims. In this context, there is general consensus that an effective silvicultural method to reduce insect damage is to mix tree species (65, 102). A recent meta-analysis of over 600 case studies showed that, overall, a tree species grown in a mixed stand is less likely to be damaged by a given insect species than one grown in a pure stand, with an average reduction in damage of approximately 23% (67). This so-called associational resistance (11) has been confirmed for most insect guilds, including wood-borers, chewers, leaf-miners, gall-makers, and sap-feeders. However, the magnitude of associational resistance is greater against specialist insects than against generalists. In addition, the resistance of mixed stands does not depend only on the number of tree species, but also on the dissimilarity of co-occurring tree species. In particular, mixing broadleaf and conifer species appears to be a promising approach to reduce pest damage on conifers. Concerning the relative proportion among different species, the level of damage to a focal species in a mixed stand decreases with the relative proportion of companion tree species (there is a significant reduction when companion tree species make up >30% of the stand; 67). Monospecific forests still represent approximately one-third of the total global forest area (42), and these forests are expected to have higher susceptibility to insects and lower ecosystem resilience to climate change due to the dominance of single tree species (29, 100, 108).

Associational resistance: decreased herbivory experienced by a focal plant growing among neighboring individuals belonging to different species

2.2. Use of Genetically Resistant Trees

There have been recent calls (97, 124, 129) for increased efforts to develop tree breeding programs and deploy genetically resistant tree varieties to counter threats of insect outbreaks in response to climate change and biological invasions. At present, successes remain scarce (e.g., with Sitka spruce) and largely hypothetical (2, 17, 134), and the remaining obstacles (56) make it doubtful that genetically improved tree resistance will soon be of practical relevance. Difficulties include the diversity of interactions between trees and multiple pest species and the diversity of potential resistance mechanisms (e.g., avoidance, nonpreference, antibiosis) (134). The challenge is exacerbated by the continuing appearance of non-native pests, as in the case of ashes in North America. A further problem is the durability of tree resistance to organisms that can produce tens to hundreds of generations over the life span of trees and are therefore likely to evolve counter-resistance, as has already been observed in perennial *Bacillus thuringiensis* (Bt) crops within a decade of their implementation—even with the inclusion of non-Bt crop refugia (136). At least at present, maintaining natural genetic diversity that enables tree populations to evolve in response to rapid changes in the abiotic and biotic environments seems more promising than the large-scale propagation of resistant clones or varieties (40, 137).

2.3. Site Selection and Matching with Future Climate

Forestry has often involved the propagation of economically valuable tree species outside of their native geographic range, which sometimes involves suboptimal climatic conditions (e.g., too warm and dry). Recent reviews have shown that water-stressed trees are generally more susceptible to insect attacks but have also noted that damage to trees depends on the intensity of drought and the guild of insect herbivores (52, 69). Moderate or intermittent water stress is likely to increase carbon-based chemical defenses (57) that are unfavorable to bark and wood borers, whereas an increase in nitrogen concentration would favor leaf chewers. Under severe or prolonged drought, tree leaves are more difficult to chew and contain fewer nutrients and are thus less suitable to insect defoliators, sap-suckers, and leaf-miners, whereas tree trunks and branches are less well defended and therefore more prone to bark beetle infestations (60, 88, 91). Thus, it is widely advisable to plant or regenerate the tree species best adapted to current and future climatic conditions. In particular, considering the available projections of climate warming, we should consider adjusting the tree species composition to more warmth- and drought-tolerant species to sustain ecosystem functioning in the long run (120). Foresters have also planted several non-native trees in response to the emerging challenges associated with climate change, with the idea that exotic trees are also less vulnerable to native pests. However, several studies found similar vulnerability of native and exotic trees to native phytophagous species, also indicating an increasing risks of native pest adaptation to exotic hosts over time (e.g., 19).

Less research has been done on the effects of soil fertility on the resistance of forest stands to insect attacks (15) and how this can be modified through fertilization. The few studies that compare insect pest attacks on fertilized and nonfertilized trees often provide contradictory results (63, 92, 105). Despite this variability, it appears that high N fertilization frequently promotes pest attacks, especially in boreal regions where fertilization is sometimes applied in managed forests (101).

2.4. Natural Regeneration versus Plantation

One important decision of forest managers is the choice of tree propagation methods, which can range from natural regeneration to planting with intensive postplanting care. While economic or environmental criteria often prevail for this choice, it can also be dictated by a wish to minimize phytosanitary risks. Generally, the main biotic hazards at the regeneration stage are grazing or browsing by large herbivores, but some insects, like weevils (e.g., *Hylobius* spp.) or shoot moths (e.g., *Rhyacionia* spp.), also target seedlings or saplings. The literature on this topic is scarce and provides mixed results (113). Regeneration methods that favor greater height in the seedlings are more likely to attract primary pests (102). While natural regeneration often leads to higher densities of seedlings, leading to an increased risk of colonization by insect herbivores (115), this higher density offers more options to find undamaged trees during subsequent thinning operations. In the case of artificial regeneration, mechanical preparation of the planting site, including soil scarification, soil inversion, and tillage, can sometimes reduce seedling mortality (125). Stump and slash removal can also contribute to lower damage on spruce seedlings (110) and reduce the risk of outbreaks of bark beetles such as *Pityogenes chalcographus* (48) and *Hylaste*s spp. (110). However, the removal or destruction of logging residues can lead to loss of nutrients and biodiversity and should therefore be applied with caution, for example, by choosing the right size and age of residues to be managed.

Thinning: practice of reducing tree density through selective cutting of young stands

Forest rotation: production cycle of a forest from the regeneration stage to the harvest, usually referring to clear-cut systems where all the trees are cut simultaneously

2.5. Tree Density Reduction

Thinning of conifer stands is commonly recommended in North America to improve forest resistance to bark beetle attacks. Reducing the basal area within pine stands is demonstrably effective against many North American scolytids such as *Dendroctonus ponderosae*, *Dendroctonus frontalis*, *Dendroctonus brevicomis*, and *Scolytus ventralis* (39, 44, 62, 98, 104, 153). The number of pine trees attacked by the European wood wasp also decreases with reduced basal area (76). However, thinned stands actually permitted higher reproductive success of pine engravers, suggesting that differences among bark beetles can alter their responses (59). Surprisingly, to our knowledge, thinning has not been explicitly tested for pest management in European forests. However, thinning usually leads to increased spacing among host trees, impeding the aggregation behavior that underlies mass attacks and reducing competition among trees for light, water, and nutrients (4). It has been suggested that thinning is more effective in preventing the rise of outbreaks in endemic populations of bark beetles than in limiting damage once an outbreak is happening, and it is not clear if thinning is equally effective for pest management in systems outside of conifers and bark beetles (45, 139, 144). For the case of canopy defoliators, there is evidence that thinning can actually exacerbate damage. For example, the density of sawfly larvae (107), the percentage of trees attacked by the pine processionary moth (111), and the growth performance of spruce budworm caterpillars (50) were all higher in thinned forests, probably because of increased success in host location by insects and/or improved leaf quality. In some cases, the increase in insect defoliation did not exceed the gain in foliar production due to reduced competition between trees, which resulted in an increased capacity of thinned trees to tolerate further attacks by defoliators (12).

2.6. Stand Age

The often observed positive relationship between forest age and vulnerability to insects suggests that a reduced forest rotation length can reduce the impacts of several wood-boring species (5, 10, 13, 29, 133, 147, 154). This effect is particularly strong for bark beetles, where the positive age effect is often related to preferences for large-diameter trees, which have more space and phloem resources for ovipositing adults and feeding larvae (4, 79). Similar results were also found for sap-feeders and chewers, where the most severe impacts were observed in the oldest stands and/or on large trees that were retained beyond the normal rotation age (111, 135). Several mechanisms can explain the effect of forest age, including differences in microclimate, increased diversity of natural enemy communities, or changes in the leaf nutritional quality or defenses (78). However, a unimodal relationship between tree age and insect damage, in which middle-aged trees are preferred, has sometimes been observed (4, 24). In addition, stands that contain a mixture of trees that vary in age and size are expected to be less vulnerable to insect outbreaks as a consequence of more dispersed hosts that are less easy for insects to locate (135).

Landscape composition: proportional cover of the different habitats that are relevant to the organisms under consideration

Landscape configuration: refers to the spatial arrangement of the habitat patches, including various spatial characters such as shape, connectivity, and geometry

Resource concentration hypothesis: denser or larger stands of a host plant recruit more herbivores per unit plant; these herbivores will also feed for a longer time than they would on isolated host plants

Connectivity: the degree to which a landscape facilitates the movement of individuals among suitable habitat patches

2.7. Forest Fuel Reduction

In some temperate and boreal regions dominated by conifer forests, bark beetle outbreaks and wildfires can interact in complex ways to shape natural forest dynamics. Fire injuries usually increase the susceptibility of trees to attack by bark beetles, and when pest populations are locally abundant, postwildfire mortality is common (84). Therefore, short-term increases in levels of bark beetle–caused tree mortality are often reported following prescribed fire (132). However, in the long term, burned areas may benefit from prescribed fire due to the increased growing space and lower competition among trees, which can contribute to reducing forest susceptibility to bark beetles (46, 47, 70). A common concern is that fire-injured, attacked trees may serve as sources of bark beetles that can later colonize adjacent trees in high-density stands, but this has not been well documented (83, 132). Although more research is needed, it appears that there may be little long-term difference in tree mortality from bark beetles between untreated stands and those subjected to fuel reduction treatment (149).

2.8. Take-Home Message

For most forest types, local stand management practices appear to cause idiosyncratic effects on pest damage depending on the environmental context and the focal pest species. However, increasing tree diversity within stands appears to be a general strategy for reducing pest damage.

3. EFFECT OF LANDSCAPE PROCESSES

In addition to the local effects described in the previous section, forest management shapes the compositional and the configurational heterogeneity of landscape mosaics by changing the size and type of forest stands that constitute them (41). Only recently has the importance of landscape processes gained attention in forest entomology and forest management (43, 121, 150), and several studies have started exploring the effects of both landscape composition and landscape configuration on insect population dynamics and outbreak propensity (**Figure 1**).

3.1. Host Concentration Across the Landscape

The resource concentration hypothesis predicts that herbivory should increase with the density of host plants (115). If we upscale this mechanism, then insect damage is predicted to increase with increased host concentration across the landscape (24). The most destructive large-scale outbreaks recently observed across Europe and North America can be partially explained by the large availability of forests with uniform age and tree composition combined with the ability of larger regional insect populations to overwhelm tree defenses (6, 29, 60, 71, 141). It has been reported that a greater proportion of preferred host trees in the surrounding landscape increases local defoliation severity (5, 23, 24, 85, 117) and can be associated with large-scale outbreaks (87, 109). In addition, dispersal of herbivores should increase with increasing connectivity between stands, a feature that would tend to maximize colonization success (112, 116). An increase in the scale of host concentration across the landscape is therefore a key risk factor for outbreaks of specialist insects. However, extreme resource isolation at the landscape level may sometimes cause some insect species to dedicate more time to foraging within small resource patches, thus increasing local damage in isolated stands (22, 148). The few studies incorporating a longer temporal perspective have found complex interactions between host fragmentation and insect population dynamics. For instance, spruce budworm outbreaks are of higher frequency and lower intensity and are less spatially synchronized in more fragmented, younger forests with a lower proportion of host species than in regions with older forests and more concentrated host species (114). The mountain pine beetle also displays different population dynamics that are related to fragmentation: Fragmented forests experience greater tree mortality than contiguous forests when beetle populations are low but experience less damage during outbreaks (16, 26). There remains much to be discovered about how host concentration influences density-dependent feedback in the population dynamics of forest insects.

Heterogeneous landscape: a geographic area characterized by diverse interacting habitat patches, ranging from relatively natural habitats such as forests or grasslands to human-dominated habitats such as agricultural and urban elements

Edge density: length of the habitat margin standardized per unit area; usually refers to a single habitat (e.g., forest, urban)

3.2. Landscape Heterogeneity

Studies testing the resource concentration hypothesis commonly assume a simple dichotomy between suitable habitat where the host is present and the matrix composed of unsuitable habitats. This approach can discount potential effects stemming from the variety of resources that can occur across heterogeneous landscapes composed of different habitats and forest types (89). This is particularly relevant for temperate and tropical regions, where landscapes can exhibit a large diversity of forest types and age structure at relatively small spatial scales. The pervasive effects of forest diversity on insect herbivores found at the local scale (67) suggest that similar effects of forest heterogeneity could also work at larger spatial scales (28). Indeed, it has been reported that the movement of insect populations and their colonization of forest patches can be slowed down by landscape diversity (99, 112). Just as neighboring nonhost trees can act as physical or chemical barriers to the colonization of individual host trees (36, 111), the presence of forest patches with high concentrations of nonhosts may also impede or reduce successful colonization of suitable stands at the landscape scale (21). For instance, the frequent presence of a less palatable host tree species across the landscape can decrease the local damage during outbreaks (23). In addition, populations of vertebrate natural enemies such as birds and bats are expected to increase with landscape heterogeneity (25). Moreover, the few studies investigating multiple spatial scales found strong scale dependence in the effect of landscape diversity on insect damage, suggesting that different ecological processes may act at different scales (8). High landscape diversity has also been shown to decrease outbreak duration; i.e., the likelihood of a single year of defoliation is greater in highly diverse landscapes, while the likelihood of sustained multiyear defoliation is higher in homogeneous landscapes (24).

3.3. Landscape Configuration

Besides the research on the effects of host connectivity described above, there are very few studies that have empirically evaluated other aspects of landscape configuration, such as the degree of fragmentation or the shape and size distribution of forest patches. Early modeling studies suggested that the effects of landscape configuration can be as important as those of landscape composition in affecting dispersal mortality among suitable habitat patches and altering host–parasitoid interactions (64). However, the few empirical studies on landscape configuration available found that edge density was not important in explaining local forest mortality, which implies that habitat configuration was relatively unimportant compared to host concentration (126). As in the case of the better-studied crop insects, configurational aspects of landscape structure might affect forest insect suppression by modifying the spillover of organisms along the interface between different habitat patches and the accessibility of resources across heterogeneous landscapes (41). Landscape ecology theory suggests that these configurational effects should, however, be important mostly in landscapes where forest is not the dominant land use or when habitat diversity is high.

Salvage logging: practice of logging trees in forests that have been killed or damaged by biotic and abiotic disturbances to recover economic value

Sanitation logging: practice of cutting and removing trees that have been attacked by a pest or a pathogen to prevent the attacker from spreading to other nearby trees

3.4. Take-Home Message

Although landscape ecology of forest pests is still an emerging field of research, available studies indicate that increasing the diversity of forest types and age structure at large spatial scale seems to reduce the probability and duration of large-scale outbreaks.

4. REACTIVE FOREST MANAGEMENT

In this section, we review control measures based on tree and stand management to contain ongoing outbreaks. We do not consider several other common direct control measures, such as the use of pesticides (61), semiochemicals (123), mass trapping, or classical biological control (74).

4.1. Removal of Dead and Damaged Trees: Salvage Logging

Salvage logging is one of the most widespread reactive responses to forest disturbances across temperate biomes (81). Salvage logging consists of the removal of damaged trees in disturbed forests with the primary intention of regaining economic losses and reducing ecological hazards. It is well known that high availability of storm-felled trees can trigger outbreaks of several bark beetle species such as *Ips typographus* L. (91), *Tomicus piniperda* L. (106), and *Dendroctonus pseudotsugae* Hopkins. The main mechanism to prevent or slow down the buildup of these insects is the removal of breeding material for future generations. Despite widespread applications of this practice after snow or wind storms, solid scientific evidence of its effectiveness is still doubtful (30, 80, 128). In Europe, recent simulation models show that the effectiveness of the removal of wind-felled trees with the intention of preventing bark beetle outbreaks critically depends on a high intensity of removal (e.g., >90%; 31). This may be because the disturbance events are commonly large scale and produce a vast resource supply relative to low initial abundance of the insect (91). Besides the intensity of the removal, the spatial configuration of the removed wind-felled trees seems to play a role in affecting insect populations; i.e., focusing logging on the vicinity of roads or creating large blocks of treatment area can contribute more effectively to reducing outbreaks (32). Recent studies in North America found no evidence of alarming population increases of primary bark beetles after storms even with no salvage logging, suggesting that salvage operations are not always necessary to protect residual trees from attack by destructive bark beetles (35).

4.2. Removal of Infested Trees: Sanitation Logging

Another frequent practice to reduce the negative consequences of ongoing outbreaks is to swiftly remove attacked trees (i.e., sanitation logging or sanitation felling). The timing of these operations is crucial due to the usually short period of time between detection of tree symptoms and the emergence of adults from the attacked trees. In Europe, sanitation felling is a routine management practice in the control of *I. typographus*. The few long-term studies investigating spatiotemporal dynamics of insect outbreaks indicate mixed results. In some cases, sanitation felling appeared to reduce the emergence of new infestations, although the effect was generally small compared to the costs of such interventions (131). However, the removal of bark beetle–attacked trees in European forests has been more commonly reported to have had no impact or sometimes even to have increased tree mortality (73, 94). The situation differs in North America, where active suppression tactics have proven to be effective in managing local and landscape outbreaks of the southern pine beetle. In the most effective version of southern pine beetle suppression, the pine trees that are currently infested or presently coming under attack are rapidly cut and removed from the forest (14). This reduces the local abundance of beetles and, perhaps most importantly, eliminates the pheromone plumes that permit the successful mass attack of host trees. These tactics can reduce tree losses to southern pine beetle up to 85% (14, 34). Cut-and-remove suppression has not generally been feasible for congeneric mountain pine beetle in the Rocky Mountains, but it has shown promise where it was possible to implement (27).

4.3. Nonintervention Strategy

Based on the results outlined above and considering the potential negative effect of salvage and sanitation logging on biodiversity and ecosystem services, some authors have advocated for a strategy of nonintervention (54). Nonintervention allows natural tree mortality and does not interfere with the complex biotic interactions among host tree, herbivores, and natural enemies. For instance, host competition and epizootics can reduce risks of long-term outbreaks even under a nonintervention management strategy (90, 91). In several protected areas, managers have already adopted this nonintervention strategy due to management restrictions in some biodiversity conservation areas. Thus, several studies compared insect outbreak dynamics within and outside protected areas (especially with respect to *I. typographus* in Europe). The comparisons between managed and unmanaged forests indicate that multiple practices aimed at mitigating tree mortality have been largely ineffective (77, 94, 146). It is important to stress, however, that most studies to date have compared managed and unmanaged areas separated by distances less than the dispersal capacity of the pest insect (142). Moreover, it is well known that unmanaged disturbed forests can deliver multiple ecosystem services including biodiversity (140), carbon storage (118), and soil and water protection (53).

4.4. Take-Home Message

For most forest systems, there is little support for the implementation of reactive emergency measures for suppressing insect outbreaks. This is due to both low effectiveness for pest control and negative impacts on other ecosystem attributes such as biodiversity and soil stability. A notable exception is the frequently successful control of the southern pine beetle in North America via rapid cut-and-remove suppression.

5. THE WAY FORWARD

5.1. Looking for Compromises

One of the main difficulties in designing forest management to reduce the vulnerability of stands to damage by insect pests is that the target tree species is exposed to multiple pest species that occur simultaneously or successively during the forestry cycle and have various modes of interaction with the host tree. Consequently, a single silvicultural operation can prevent attacks by one insect species but favor another or increase vulnerability to other hazards (68). It is therefore advisable to find compromises that take into account the pleiotropic effects of silvicultural actions on the susceptibility of forest stands to different disturbances so as to reduce the cumulative damage suffered throughout the whole period of management. Finally, not all forest damage has the same socio-economic consequences for the managers; the consequences depend on the values at stake and the nature of the damage. To take all these aspects into account, it would be useful to generalize multicriteria risk analyses (66, 80). This method, based on expert opinion, allows classification of different stand management alternatives according to their effect on single-stand vulnerability to different pests and weighting of these criteria according to the frequency or intensity of their infestations.

5.2. Moving from Resistance to Resilience Management?

Forest resistance is the ability of the forest to avoid or reduce the negative impact (e.g., loss of biomass) related to herbivores, while resilience reflects the amount of damage that an ecosystem can withstand before there are irreversible shifts or state changes (55). Although most of the research on forest insects to date has focused on increasing forest resistance, the idea of changing forest management to improve resilience might be attractive for local stakeholders and managers in the face of the great uncertainty related to global change. However, while the concept of resilience is apparently simple, there are few explicit guidelines on how to assess and manage for resilience in forests (1, 62, 103). As biotic and abiotic disturbances can occur across a range of temporal and spatial scales, the central question is how to identify the scale at which to pursue forest resilience (**Figure 2**). On the one hand, across heterogeneous landscapes, single forest stands can abruptly change as a result of local outbreaks without affecting the whole system. On the other hand, in homogeneous landscapes where the scale and duration of the outbreak become too large, the system has the potential to collapse or go beyond the threshold of sustainability (95, 119). Several studies on post-outbreak recovery indicate that the functioning of forests can be relatively resilient to

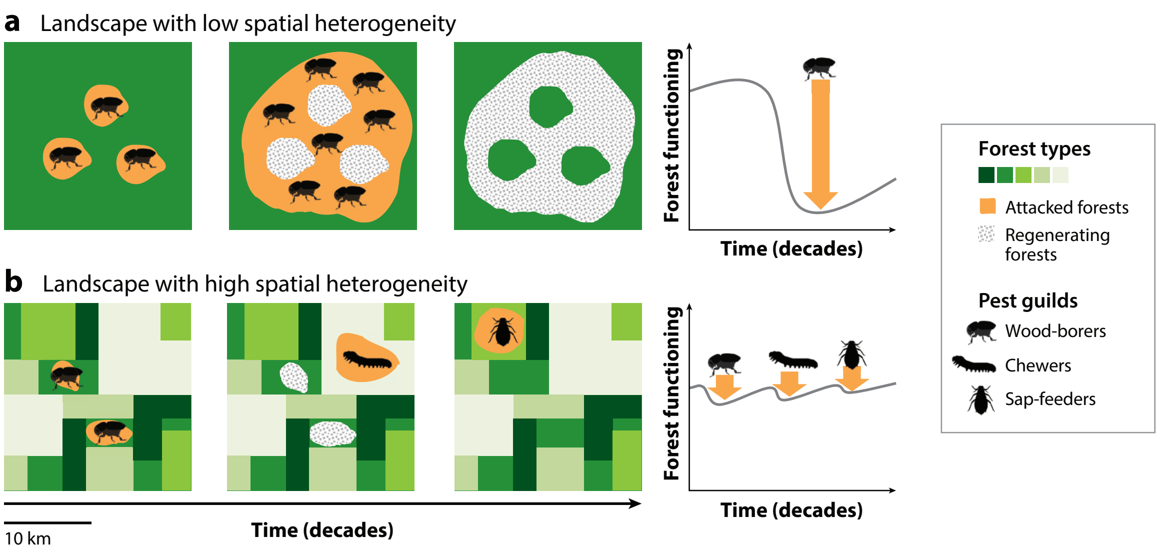

Figure 2

Expected effects of landscape heterogeneity on insect damage. (*a*) In highly homogeneous landscapes dominated by single tree species, there are high chances of large outbreaks causing quick pulses in forest biomass, while (*b*) in heterogeneous landscapes with multiple forest types, insect disturbances are expected to be smaller and shorter, maintaining higher stability in ecosystem functioning at a large spatial scale.

insect outbreaks (20, 96), but the economic losses are sometimes so great that they promote land use changes from forest to other land uses. It could be expected that large homogeneous forest landscapes are at greater risk of irreversible state changes from forest pests.

5.3. Reconciling Better Resistance and Resilience with Other Forest Management Objectives

Forest ecosystems deliver multiple services, including timber production, carbon sequestration, biodiversity, health and recreation, water supply and quality, and flood protection. Fortunately, most of the management interventions aimed at increasing stand and landscape diversity are also expected to improve other key ecosystem services (9, 51, 127). However, one prominent negative trade-off between provisioning services and forest resistance often occurs in management-intensive timber production forests, where specialization and market demands have often contributed to the creation of large homogeneous stands that are highly productive but, at the same time, highly susceptible to insect attacks and other disturbances (29, 143). When clear negative trade-offs between provisioning services and forest resistance emerge (138), we recommend a diversity of management approaches at relatively small spatial scales that tend to promote resilience and maintain desirable ecosystem services at the regional scale.

6. CONCLUSION: THE IMPORTANCE OF MAINTAINING SPATIAL HETEROGENEITY AT MULTIPLE SPATIAL SCALES

Our review supports the emerging consensus that insect outbreak dynamics are a product of multiscale processes (109) and that forest management to mitigate the impacts of insect disturbances should consider landscape- and regional-scale factors in addition to stand-scale factors (86, 122). Managing tree species diversity at the stand level appears to be an effective general approach for preventing forest pest infestations and damage, while the effects of single silvicultural practices are frequently idiosyncratic depending on the environmental context and the focal pest species. Our review also indicates that managing spatial heterogeneity at the landscape scale should be considered a new frontier to improve forest resistance and resilience against biotic disturbances (**Figure 2**). These systems, however, require that land managers understand the ecological processes that operate at large spatial and temporal scales, including the pivotal role that forest insects can play in forest dynamics. Although we still lack the capacity to routinely track outbreak dynamics of forest insects at a spatial and temporal resolution suitable for conducting landscape-scale analyses, recent advances in remote sensing, such as the use of Landsat or Sentinel satellite images, can strongly improve our understanding of landscape-scale processes (93). In particular, the risks of overconnected, highly conductive systems of susceptible monospecific forests call for a multiscale approach to pest management (150). In forest landscapes that contain little heterogeneity due to the presence of large contiguous pure stands, forest managers can promote practices that increase landscape heterogeneity in terms of forest type, tree age, and species composition (45). The necessarily large scale of such practices suggests the need for communication, cooperation, and coordination among multiple forest owners and stakeholders. Natural disturbances can be a benefit when they create mosaics of different disturbance histories and promote heterogeneity across forest landscapes (49, 80). Heterogeneous forest systems can accommodate a range of ecosystem functions and services (51), including the sometimes-antagonistic hopes from society for forest products, biodiversity, and other ecological values (3). Diversifying forests at multiple spatial scales to reduce forest health risks is possible (33, 38, 58) and does not heavily compromise economic viability; consequently, it can effectively improve socio-ecological resilience of forest ecosystems. Finally, while current policy directions still favor intensive reactive management in forests attacked by insect pests, we recommend a change in policy to allow more natural disturbance dynamics to operate as a useful conservation tool, in particular in regions characterized by largely homogenized forest landscapes. The frequent high costs and low efficacy associated with salvage and sanitation logging suggest that a nonintervention strategy should be prominent within the portfolio of possible management solutions.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Research was supported by the HOMED project, which received funding from the European Union's Horizon 2020 research and innovation program under grant agreement 771271 and U.S. National Science Foundation Long-Term Ecological Research award 1637685.

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