Landscape Ecol (2021) 36:945–972
https://doi.org/10.1007/s10980-021-01209-7

REVIEW ARTICLE

Global review on interactions between insect pests and other forest disturbances

Quim Canelles · Núria Aquilué · Patrick M. A. James · Joshua Lawler · Lluís Brotons

Received: 29 June 2020 / Accepted: 1 February 2021 / Published online: 23 February 2021

Abstract
Context Forest landscapes worldwide are shaped by abiotic drivers such as fire, windstorms, and drought, but also by biotic drivers like insect pests and pathogens. Although the effects of such drivers on forest dynamics have been studied extensively, knowledge of the interactions between insect pests and other drivers of change is still coarse and fragmented. Indeed, new invasive insect species and global change may lead to novel interactions and produce impacts on forest ecosystems never before experienced.
Objectives We aimed to review the mechanisms underlying interactions between insect pest outbreaks and other forest disturbances, identify interactions emerging from current disturbance dynamics, and highlight the role of simulation models in exploring these interactions in a dynamic, mechanistic, and spatially explicit manner.
Methods We reviewed the state of the science regarding interactions between insect pests and other forest disturbances, collecting a set of 216 scientific articles.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10980-021-01209-7.

Q. Canelles · N. Aquilué · L. Brotons
InForest Jru (CREAF-CTFC), Crta. de Sant Llorenç de Morunys, Km. 2, 25280 Solsona, Spain

Q. Canelles (✉)
Centre de Ciència i Tecnologia Forestal de Catalunya, CTFC, Crta. Sant Llorenç de Morunys, km 2, 25280 Solsona, Spain
e-mail: quim.canelles@ctfc.cat

N. Aquilué
Centre for Forest Research (CFR), Université du Québec à Montréal (UQAM), C.P. 8888, succ. Centre-Ville, Montreal, QC H3C 3P8, Canada

P. M. A. James
Institute of Forestry and Conservation, University of Toronto, Toronto, ON M5S 3E8, Canada

J. Lawler
School of Environmental and Forest Sciences, University of Washington, Seattle, USA

L. Brotons
CREAF, Campus de Bellaterra (UAB) Edifici C, 08193 Cerdanyola del Vallès, Spain

L. Brotons
CSIC, 08193 Cerdanyola del Vallès, Spain

Results Most studies focused on the interaction between insect outbreaks and fire, whereas interactions between insect pests and drought, forest management or forest diseases received much less attention. Although we identified some trends in how interactions were manifested, interactions were not more commonly found at particular spatial or temporal scales. Relatively few studies used simulation models to explore interactions between disturbances and very few studies explored multiple interactions.
Conclusions Interactions between pests and other forest disturbances play critical roles in driving forest dynamics. The effects of these interactions are likely to increase in the face of continuing global change.

Keywords Simulation modeling · Outbreak · Fire · Drought · Climate change · Landscape dynamics

Introduction

Forest disturbances such as fire, drought, windstorms, landslides, disease, and insect outbreaks are key drivers of change in forested landscapes. Disturbances modulate landscape dynamics by modifying forest composition and structure, influencing forest ecosystem functioning and resource availability (White and Pickett 1985; Seidl et al. 2017), and facilitating adaptation to new environmental conditions (Thom et al. 2017). Despite the essential role that natural disturbances play in forest ecosystem functioning and composition, our understanding of their future impacts remains limited due to the complex feedbacks that exist between disturbances and global change (Dale et al. 2001; Turner 2010). For instance, ongoing changes in the global economy, land use, and climate change may lead to more extreme disturbances (such as windstorms, floods, and wildfires) with yet unknown consequences for forest landscapes (Weed et al. 2013; Duane and Brotons 2018). Such changes may also result in novel disturbance caused by invasive species introduced via international trade (Brockerhoff et al. 2006; FAO 2008; van Lierop et al. 2015).

Insect pests are one of the main agents shaping forest landscapes, affecting almost 35 million ha annually, mainly in boreal and temperate biomes (van Lierop et al. 2015). Although many native pests and diseases are integral agents of forest ecosystems, high-intensity outbreaks can have adverse effects on tree growth and survival (van Lierop et al. 2015). The extent and subsequent economic and ecological costs of pest outbreaks have increased in recent decades as world trade has facilitated the spread of invasive species (Hulme 2009; Turner 2010).

Insect pests are highly sensitive to global change. New environmental conditions resulting from changes in temperature, precipitation, and drought can alter insect development and reproduction (Ayres and Lombardero 2000; Kingsolver et al. 2011), and hence population dynamics and outbreaks. These changes may also enable native and invasive insect pests to spread to areas currently free of such outbreaks (Cullingham et al. 2011). Changes in land use can also influence insect population distributions and local viability (Rosenberger et al. 2017). Although the impact of direct climate-pest and land-use-pest have been examined, we know less about the indirect consequences of insect pests on forest ecosystems through their interactions with other disturbances (Ayres and Lombardero 2000; Raffa et al. 2008; Hessburg et al. 2015).

A deeper understanding of forest disturbance dynamics and their interactions is required to better forecast how global change will affect forest ecosystems (Buma and Wessman 2011). Insect outbreaks have complex relationships with other disturbances, and can be affected by fire (Parker et al. 2006; Chou et al. 2010; Hicke et al. 2012; Jenkins et al. 2014), drought (Sangüesa-Barreda et al. 2015; Temperli et al. 2015), windstorms (Reyes and Kneeshaw 2008; Potterf and Bone 2017), forest management (Bauce and Fuentealba 2013; Rosenberger et al. 2017), pollution (Roth et al. 1998; Agrell et al. 2005), and other pests or diseases affecting the forest (Jones et al. 2015; Borkowski and Skrzecz 2016). Many studies have explored the interactions between insect pests and other disturbance agents (Colgan and Erbilgin 2010; Day and Pérez 2013; Gitau et al. 2013; Anderegg et al. 2015; Millar and Stephenson 2015; Kolb et al. 2016; Agne et al. 2018; Leverkus et al. 2018). However, to date, no global synthesis exists that integrates such interactions with insect pests across different agents and regions, analyzing how global change may influence these interactions in the near future (Seidl et al. 2011), or how alterations in current ecosystems may lead to novel interaction regimes (Turner 2010). Such a synthesis is challenged by the diversity of insect feeding strategies and outbreak dynamics, the multiple ways in which one can characterize insect outbreaks (e.g., severity, frequency, extent), and the multiple spatiotemporal scales at which disturbance interactions occur (Joseph et al. 2001; Hanula et al. 2002; Meigs et al. 2015, 2016; Kelsey and Westlind 2017a).

Ecological models are essential for improving our understanding of interactions between pests and other disturbances in the face of rapid global change. Although empirical models (based on statistical relationships among drivers and a response variable; Table 1) are widely used, they can only model observed dynamics and are therefore limited in their capacity to make predictions in novel contexts. In contrast, simulation models (mechanistic models based on a combination of theoretical understanding and mathematical/empirical information; Gustafson and Keene 2014) can be designed to include the effects of uncertain, multiple interacting disturbances characterized by cumulative effects, non-linear dynamics, cross-scale interactions and, most importantly, with the potential to capture unobserved dynamics (Clark and Gelfand 2006; Ager et al. 2007; Taylor et al. 2009; Baker and Robinson 2010; James et al. 2011; Keane et al. 2015; Maroschek et al. 2015; Leite et al. 2018). Such simulation models are particularly appropriate methods to assess changes in insect species ranges, predict novel insect outbreaks, and anticipate host–insect relationships under novel environmental conditions (Taylor et al. 2009; Maino et al. 2016; Barbet-Massin et al. 2018).

Here we present a systematic review of spatiotemporal interactions between insect pest outbreaks and other forest disturbances. We aim to: (1) detail the processes that determine how insect pest outbreaks interact with other disturbances, while highlighting the main sources of variability in such interactions; (2) identify current and potential future interactions between insect pests and emerging disturbances in the face of global change; and (3) discuss the role of simulation models as a tool for studying both current and novel forest disturbance interactions.

Methods

We searched for publications that examined interactions between insect pests and other forest disturbances. We used the Web of Science, Scopus, and Google Scholar databases to identify articles published between 1990 and 2019 that contained the following words in the title, abstract, or keyword: (Insect) AND (outbreak* OR defoliat* OR infest* OR pest OR bio* disturb* OR epidemic*) AND (forest* OR tree* OR landscape* OR stand*) AND (*fire* OR *burn* OR *drought* OR *logging* OR forest management OR harvest* OR *wind* OR hurricane OR *snow* OR *storm* OR *flood* OR *slide* OR disease OR *pollution*) AND (interact*).

We defined an interaction between disturbances as a direct or indirect relationship in which one disturbance affects the likelihood, extent, severity, or impacts of another. These effects could be either synergistic (a disturbance favors the likelihood or accentuates the impact of a subsequent disturbance) or antagonistic (a disturbance hinders, reduces, or prevents the likelihood or impact of a subsequent disturbance). We did not explicitly include climate change as a disturbance, but its effect was implicit in the influence of insect pest outbreaks, drought episodes, wildfire, wind, and flooding. Papers that were out of our thematic scope (e.g., studies focusing on agricultural instead of forest pests, or that studied multiple disturbances or climate effects on insect pests but not the interactions between them) were excluded. Finally, we included those articles that considered forest management and silvicultural interventions as drivers of change in forests, but not those that analyzed pest control via forest management. A final pool of 216 papers was selected.

We applied a common analysis scheme to all the reviewed studies. For each paper, we recorded information about the study area (at continental level), insect species examined, feeding guild (sensu Coviella and Trumble 1999; Labandeira 2013), disturbance agents involved, occurrence or lack of interaction, order of the disturbances, type of response, methodological approach, spatial and temporal scale, ecological explanation, and inferences regarding possible future trends of the interaction when applicable (Table 1). We categorized publications as being either empirical analyses or simulation modeling studies (see Table 1; Gustafson and Keene 2014). For simulation

Table 1 Information extracted from the selected articles

Parameter	Categories
Study area	Africa; Asia; Europe; North America; Oceania; South America
Insect species	Genus or species reported
Insect feeding guild	*Xylem/phloem feeders* insects feeding on the vascular tissue system (e.g., bark beetles)
	Foliage feeders insects feeding on leaves or needles (e.g., defoliators)
	Other gall producers, saproxylic feeders, seed feeders, or root feeders
Disturbance agents	Drought; Fire; Forest management; Landslides; Other pathogen/disease; Pollution; Snowstorm; Wind; Flood
Occurrence of interaction	*Lack of interaction* one disturbance has no effect on another
	Occurrence of interaction one disturbance effects another
	• *Synergistic* a disturbance increases the likelihood or impact of a subsequent disturbance
	• *Antagonistic* a disturbance reduces the likelihood or impact of a subsequent disturbance
Order of disturbances	Insect pest later influences another disturbance; Other disturbance later influences insect pest; Insect pest and other disturbance occur at the same time
Type of response	Likelihood earlier disturbance affects the probability of the later one
	Severity earlier disturbance influences the severity or intensity of the later one
	Fitness earlier disturbance influences the fitness of insect pests later in terms of reproductive success and progeny survival
	Spread earlier disturbance influences later insect spread
Methodological approach	*Empirical model approach* models assessing statistical relationships, whether causal or not, between two or more variables (also called correlative or phenomenological models)
	Simulation model approach mechanistic models built on a combination of theoretical understanding and mathematical concepts (also based on empirical information and correlative relationships) to emulate a real life system. Normally, simulation models project results to simulated future conditions. They are also called mechanistic or process-based models
Temporal scale	Days/months; 1 year; 2–9 years; 10–49 years; 50–99 years; >100 years
Spatial scale	Physiological level; Tree level (individual); Stand level (microhabitat); Landscape level
Ecological explanation	Conceptual explanation based on ecological processes that cause the interaction of different disturbances (detailed in Table 2)

The right-hand column lists in detail the different categories into which we classified each study within each information field

modeling studies, we also listed the modeling approach, the explanatory variables, the data source, and the projection scenarios considered. Information about disturbance interaction impacts (including the mechanisms of community between species, the immediate and indirect consequences of the disturbance, possible regeneration after impact, etc.) was not always available in the reviewed papers or was difficult to compare. Thus, we calculated summary statistics (frequencies) regarding the above-mentioned variables as a proxy for the incidence of interactions in ecosystems. Finally, studies that found interactions between disturbances were coded with “1”, and those that failed to find such interactions with “0”. We then used logistic regression analyses with the presence of an interaction as the binary response variable and several predictors considered to influence the disturbance interactions (i.e., disturbance agent, order of the disturbance, type of response, insect feeding guild, spatial scale, and temporal scale) as explanatory variables. Regression models were fitted using the *glm* function in R (R Core Team 2019) and significance level was considered at p-value < 0.05.

Differences in the number of publications on disturbance interaction among continents could reflect either true geographic differences in the frequency of interactions between forest pests and other disturbances, or differences in the general amount of forest research being conducted. To account for such differences, and to control for potential geographic bias, we conducted a second search in the Web of Science looking for publications on forest disturbances, in order to then calculate the ratio (per continent) of articles addressing insect pest interactions with other forest disturbances to articles only addressing forest disturbances.

Results

Geographic coverage

Most of the 216 papers reviewed addressed North American forest systems (173, 79%; Fig. 1). Of these papers, most focused on forest insects in western Canada and the USA (133, 61% of the total), followed by Europe (39, 18%). Studies from other continents were very rare and no studies were conducted in Africa.

With respect to articles that studied forest disturbances in general (those with and without interactions among disturbances), the greatest number were from North America and Europe (9931, 43% and 7453, 32%, respectively). The proportion of forest disturbance studies that addressed interactions with pests was similarly small across all continents: North America (1.73%), Europe (0.52%), South America (0.16%), Asia (0.13%), Oceania (0.07%), and Africa (0%).

Insect species

Xylem and phloem feeders, mainly bark beetles, were the most studied forest insect pests (71%), mainly *Dendroctonus* spp. and *Ips typographus* (Fig. 2).

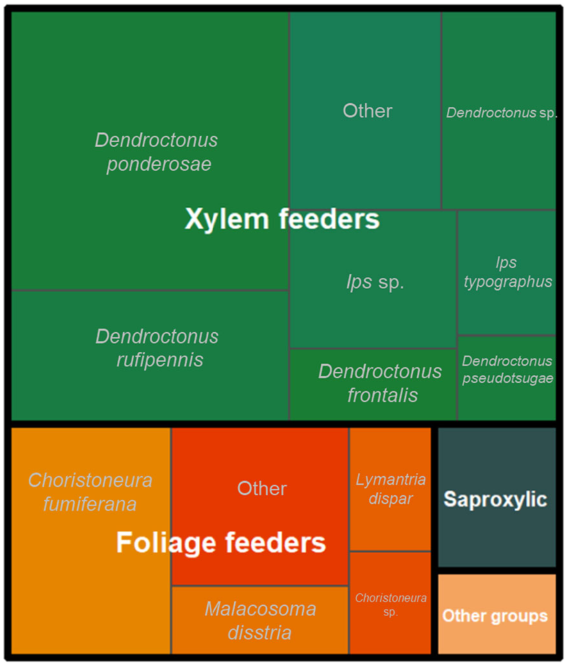

Fig. 2 Proportion of studies addressing each insect species, grouped by insect feeding guild

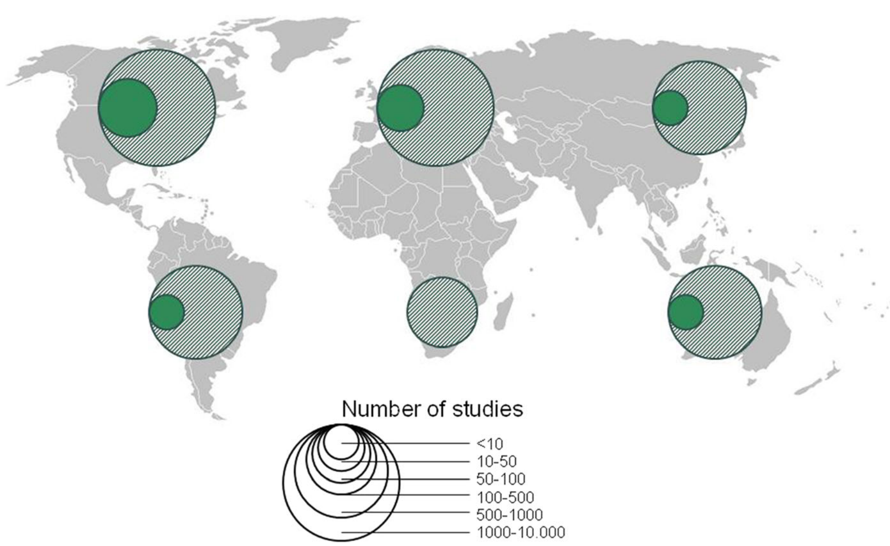

Fig. 1 Geographical distribution of number of studies at continental level. Solid filled circles indicate the distribution of the 216 papers addressing interactions between insect pests and other forest disturbances included in the review. Striped circles indicate the distribution of papers addressing forest disturbances

Foliage feeding insects such as defoliating budworms (*Choristoneura* spp.) and gypsy moth (*Lymantria dispar*) (22%), and insects of other feeding groups (7%) were also studied. We also found that interacting disturbance agents varied with insect feeding group: fire, wind, and diseases were usually associated with xylem/phloem feeders (72%, 66%, and 64% over all studies of each disturbance, respectively), pollution was mostly studied in conjunction with foliage feeders (73%). The influence of drought, forest management, and other disturbances (landslides, floods, etc.) was considered across most feeding groups.

Disturbance interactions

Interactions between fire and forest insect pests were the most commonly studied (41%; Fig. 3). Of these fire–insect studies, 48% examined how insect-induced tree mortality affects fuel loads and consequent fire activity, 36% investigated how fire promotes insect attacks, and 16% looked at how fire and insect pests together affect forest structure and composition. The second most studied interaction was with drought (24%). Such publications investigated how water-stressed trees are more susceptible to insect attacks and how insect outbreaks can increase the vulnerability of trees to moisture stress. Other interacting agents included forest diseases (11%), forest management (10%), pollution (6%), and wind and winter storm events (5%). Finally, 3% of studies examined other types of forest disturbances (e.g., landslides and floods). Although we did not explicitly include climate change as a disturbance in our list, it was considered in 48% of the papers examined.

Spatial and temporal scales

A similar number of studies focused on disturbance interactions at landscape scale (26%), stand scale (35%), and tree scale (30%), and only 9% of the studies focused on the physiological scale (Fig. 4). Simulation modeling studies tended to focus on landscapes (48%) and stands (44%) and much less on trees (8%; Fig. 5). Temporal scales covered a broad range, from a few days to hundreds of years, although most of the studies focused on interactions occurring between 2 and 9 years (36%) or 10 and 49 years (24%; Fig. 4). Longer temporal scales were more frequent in simulation model studies, where 10–49 years accounted for 60% of studies and 50–99 years 48% (Fig. 5).

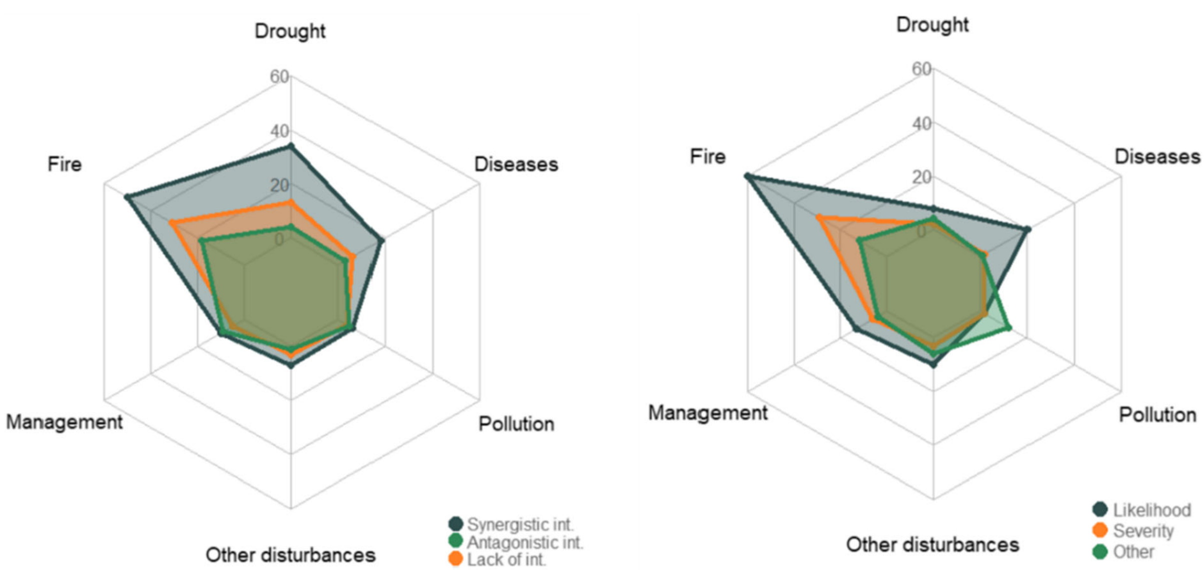

Fig. 3 Number of papers reporting synergistic interactions, antagonistic interactions, and a lack of interactions between insect pest and each type of forest disturbance (left panel). Number of papers analyzing influences on the likelihood, severity, or another type of response between insect pests and each type of forest disturbance (right panel)

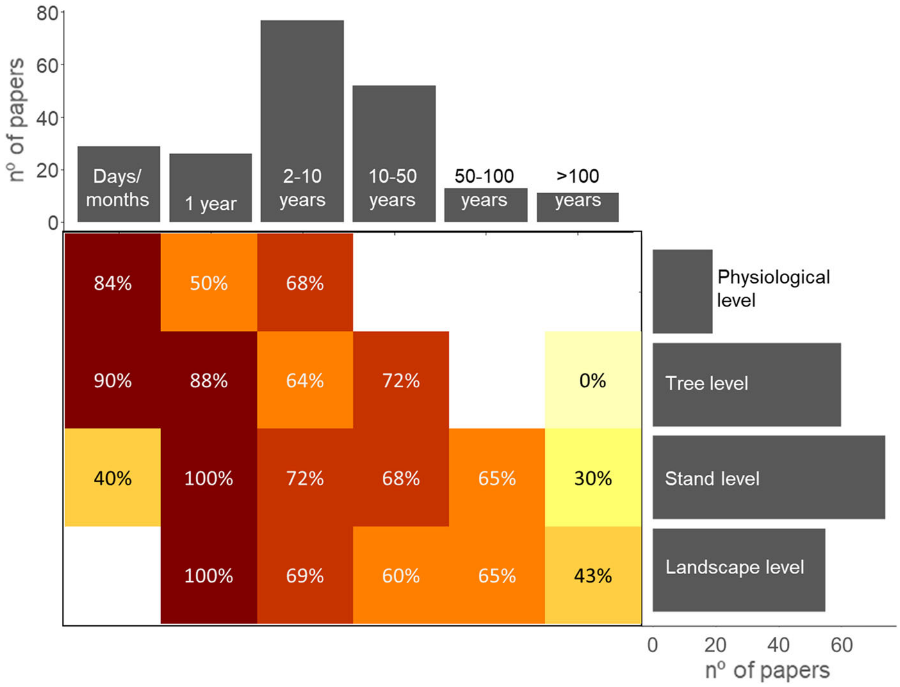

Fig. 4 Histograms of spatial and temporal scales used by reviewed studies. Heatmap indicates the percentage of interactions or lack of the interaction reported

Impact and sources of variation

Most studies reported the occurrence of interactions between disturbances (71%), considering both synergistic (54%) and antagonistic relationships (17%; Fig. 3). We found that interactions were more often identified at shorter time scales than at longer ones, while the interactions were more frequently identified at the physiological, tree, and stand scales (74%, 75%, and 71% respectively), than at landscape scale (65%; Fig. 4). However, logistic regressions showed that the presence of disturbance interactions was not significantly affected by spatial ($r^2 = 0.34$, p-value > 0.41) or temporal scales ($r^2 = 0.11$, p-value $= 0.15$). Similarly, relationships between temporal or spatial scales and the disturbance agent involved were not statistically significant ($r^2 = 0.18$, p-value > 0.06 and $r^2 = 0.14$, p-value > 0.13, respectively). However, interactions between fire and insect pests were identified more often at short, than at long temporal scales ($Z = |1.15|$, p-value $= 0.06$ and $Z = |1.03|$, p-value $=$ 0.07 at temporal scale categories 1 year and 2–9 years, respectively).

No disturbance was found to play a role in interaction occurrence more frequently than any other ($r^2 = 0.11$, p-value > 0.12 in all levels). In terms of frequencies, insect pest and forest management interactions occurred in 79% of the reviewed papers; insects and diseases, 77%; insects and drought, 74%; insects and pollution, 73%; insects and wind, 67%; insects and fire, 67%; and the two studies addressing insect pests interacting with storms and landslides also reported interactions (Fig. 3). No insect feeding guild tended to be more associated with interaction occurrence than any other ($r^2 = 0.17$, p-value > 0.91 in all levels). We also found no significant association between the occurrence of an interaction and the order of occurrence of the disturbances ($r^2 = 0.14$, p-value $= 0.31$). Nonetheless, we found that insects tended to follow fires in 57% of the reviewed studies, whereas fire followed insect pest outbreaks in 76% of the studies. We also found that the interaction of drought followed by xylem/phloem feeder insect pests occurred significantly more often than other combinations ($Z = 48.79$, p-value < 0.001).

Studies varied in terms of the specific effects of disturbance interactions they examined. For example, most of the studies reviewed (59%) investigated how an initial disturbance influences the likelihood of a subsequent one and, of these studies, disturbance interactions were successfully identified in 73% of the cases (Fig. 3). Other papers (27%) examined how a disturbance affects the severity of subsequent disturbances, finding such an interaction in 70% of cases. Finally, some studies examined how multiple disturbances affect other features, like disturbance spread (10%) or competitiveness of insect pests (4%). However, logistic regressions showed that no interaction type was more associated with interaction occurrence than any other ($r^2 = 0.13$, p-value > 0.10 for any type), neither in the case of any disturbance agent in particular ($r^2 = 0.12$, p-value > 0.06).

Simulation models and interactions between disturbances

We found 23 articles (11%) that used simulation models to investigate the interaction between insect pests and other disturbances. Again, the most frequently studied interaction was between insect outbreaks and wildfires (82%), followed by interactions with drought (35%; Fig. 5). Nine articles included three forest disturbances in a model (insect pests plus two other disturbances; Fig. 5). Almost all the models operated at either the landscape or stand scale (96%), and the most common temporal scale was 10–49 years, although some made projections over as many as 300 years. Most of the studies (63%) used previously published models (e.g., LANDIS, SORTIE, LandClim) while some built and used their own models. Many models used forest attributes (e.g., individual tree diameter, age, basal area, tree species), disturbance severity (for both insect pests and the interacting disturbance), and climatic variables as inputs. Other variables such as topography, forest spatial distribution, and soil properties were only occasionally considered. Data sources were mainly external empirical data, either from public repositories or from published studies (70%). Only in eight articles did authors compile their own data and in one case model data were simulated. With respect to scenarios, most of the studies tested models under different scenarios, either simulating different disturbance

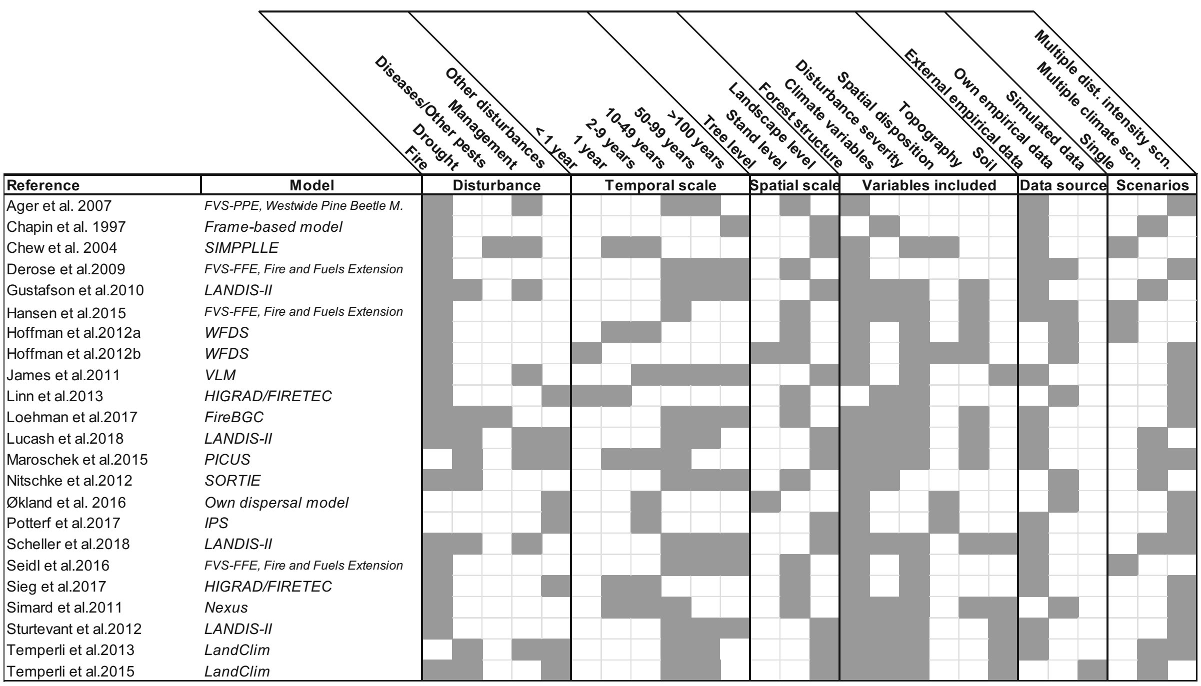

Fig. 5 Studies assessing insect pest interactions with other disturbances via simulation models showing the disturbances included, the temporal and spatial scales used, and the explanatory variables considered

intensities and/or the effects of different IPCC climate scenarios (83%; Moss et al. 2010). Finally, simulation-model studies reported finding interactions between disturbances at a similar frequency as the empirical studies reviewed here (68%).

Discussion

Global change is increasing the frequency and severity of disturbances and the uncertainty linked to disturbance interactions. Understanding forest ecosystem dynamics in such a context requires integrated research approaches that consider both individual disturbances and their interactive effects. In surveying the published literature regarding the reciprocal influence of forest insect pests on other disturbances, we found that interactions with fire and drought were the most frequently studied. We found that any of the factors considered (i.e., disturbance agent, type of response, insect feeding guild, or spatial and temporal scale) could be associated with the probability of an interaction being detected and reported in the scientific literature. Finally, simulation models were used in only 23 publications despite their enormous potential to help us further unravel how complex interactions among climate change, forest disturbance, and forest recovery processes contribute to forest dynamics and ecosystem resilience.

Geographic coverage and bias

Most studies of interactions between insect pests and other disturbances were conducted in North America and Europe. However, these two continents also produced most of the published papers on forest disturbances in general, with or without interactions. There are likely two main reasons for this, acting in combination: first, the reported absolute forest area affected by disturbances is larger in North America (followed by Europe, Africa, and Asia, respectively) than on other continents (Parker et al. 2006; FAO 2008; Weed et al. 2013). Second, as a result of economic and educational factors, scientific research output in general tends to be higher in North America and Europe (Smith et al. 2014; Gonzalez-Brambila et al. 2016).

The insect species represented in our survey reflect the geographic distribution of these studies, thus most of the insect pests studied were from North America and Europe. The most common species were those that exhibit large-scale and periodic outbreaks, such as the mountain pine beetle (*Dendroctonus ponderosae*) and the eastern spruce budworm (*Choristoneura fumiferana*), as well as other Coleopteran phloem feeders such as the North American spruce beetle (*Dendroctonus rufipennis*) and the European spruce bark beetle (*I. typographus*). These species attract greater research attention as they have large impacts on forests around the globe in terms of extent and severity, and they commonly occur in regions that are also subject to fires, drought, and forest management (FAO 2008). The economic consequences of outbreaks of these species for management agencies and the forest industry are not negligible (Chang et al. 2012). However, our findings suggest that other insect pests in other regions are understudied, such as the brown Christmas beetle (*Anoplognathus chloropyrus*) and the eucalyptus weevil (*Gonipterus scutellatus*) that interact with fires in Australia (Carnegie et al. 2005; Loch and Matsuki 2010), and the dynamics of the latter (*G. scutellatus*) also being related to drought in South Africa (Graziosi et al. 2020).

Forest disturbances interacting with insect pests

Fire: insect pests

Fire is the most studied disturbance that interacts with insect pests. Although there is a well-established hypothesis that insect attacks lead to the accumulation of more fuel and a consequent amplification of wildfire susceptibility (McCullough et al. 1998), the studies we reviewed provided mixed evidence of positive, negative, and no effect of insects on wildfire (Parker et al. 2006; Jenkins et al. 2014; Meigs et al. 2015; James et al. 2017) (Fig. 2). Studies showing evidence of insect-induced fire highlight the increase in litter (Jenkins 2011; Agne et al. 2016), crown fuel accumulation (Simard et al. 2011; Hoffman et al. 2012a, b; Jolly et al. 2012; Woolley et al. 2019), vertical connectivity (Candau et al. 2018; Crotteau et al. 2018; Watt et al. 2018), flammability of needles (Jolly et al. 2012), and wind penetration due to the lack of leaves (Linn et al. 2013) as the main drivers of the interaction, leading to high risk of ignition, spread, and severity of fire (Bigler et al. 2005; Kulakowski and Veblen 2007). Other authors did not find a positive link between

Table 2 Summary of main perturbations interacting with insect pests, their interaction cause, and its ecological explanation

Perturbation	Interaction cause	Ecological explanation	References
Fire	Fuel load and connectivity	Insect-caused tree mortality or reduction of biomass moisture content alter fuel amount and connectivity, as well as the likelihood of subsequent wildfire severity	Andrus et al. (2016), Candau et al. (2018), Chapin and Starfield (1997), Chen et al. (2017), Crotteau et al. (2018), DeRose and Long (2009), Donato et al. (2013), Flemin et al. (2002), Hansen et al. (2016), Hart, Schoennagel, et al. (2015), Harvey et al. (2013, 2014), Harvey, Donato, and Turner (2014), Hoffman et al. (2012a, b), Hummel and Agee (2003), James et al. (2011a, 2017), Jenkins (2011), Jolly et al. (2012), Jorgensen and Jenkins (2010), Klutsch et al. (2011), Kulakowski and Jarvis (2011), Kulakowski and Veblen (2007), Liang et al. (2016), Linn et al. (2013), Lynch and Moorcroft (2008), Makoto et al. (2012), McCarley et al. (2017), Meigs et al. (2015), (2016), Mietkiewicz and Kulakowski (2016), Mietkiewicz et al. (2018), Navarro et al. (2018), Page and Jenkins (2007a, 2007), Perrakis et al. (2014), Prichard and Kennedy (2014), Schoennagel et al. (2012), Sieg et al. (2017), Simard et al. (2011), Talucci and Krawchuk (2019), Watt et al. (2018) and Woolley et al. (2019)
	Attraction to the tree	Fire causes tree stress, leading to an increase of ethanol, monoterpenes and pheromones production that attract insects. Also, burned deadwood favors insect attacks	Beh et al. (2014), Coleman et al. (2008), Kelsey and Joseph (2003), Kelsey and Westlind (2017a), Liang et al. (2016), Lombardero et al. (2006), Veblen et al. (2006) and Westlind and Kelsey (2019)
	Tree susceptibility to insects	Fire weakens the defensive system of the surviving trees in terms of resins and other metabolites contributing to insect pest establishment	Amman and Ryan (1991), Bebi et al. (2003), Bradley and Tueller (2001), Chen-Charpentier and Leite (2014), Davis et al. (2012), Ehnström et al. (1995), Elkin and Reid (2004), Kulakowski and Jarvis (2013), Loehman et al. (2017), Lombardero and Ayres (2011), Lombardero et al.9 2006), McNichol et al. (2019), Pohl et al. (2006), Powell et al. (2012), Ryan and Amman (1996), Santoro et al. (2001), Schwilk et al. (2006) and Verble and Stephan (2009)
	Forest structure and composition	A first disturbance (fire or insect pest) causes changes in forest structure (in terms of age, species, understory, etc.) and favors a second disturbance (pest or fire)	Bakaj et al. (2016), Bebi et al. (2003), Bergeron et al. (1993), Bigler et al. (2005), Boucher et al. (2018), Boulanger et al. (2013), Coleman et al. (2008), Fettig et al. (2010), Hanula et al. (2002), Johansson et al. (2007), Kerns and Westlind (2013), Kulakowski et al. (2003, 2012, 2016), Lynch et al. (2006), Lynch and Moorcroft (2008), Menges and Deyrup (2001), O'Connor et al. (2015); Perovich and Sibold (2016), Seidl et al. (2016) and Stevens-Rumann et al. (2015)
	Forest consequences	Coexistence of insect pest and fire compromises forest regeneration, that is species establishment and tree growth	Burton and Boulanger (2018), Fettig et al. (2008), Harvey et al. (2013), 2014, Harvey, Donato, and Turner 2014, Hicke et al. (2015), Kulakowski et al. (2013), Land and Rieske (2006), Liang et al. (2016), Menges and Deyrup (2001), Stevens-Rumann et al. (2015), Sturtevant et al. (2012) and Vepakomma et al. (2010)

Table 2 continued

Perturbation	Interaction cause	Ecological explanation	References
Drought	Attraction to the tree	Drought causes tree stress, leading to an increase of ethanol, monoterpenes, sugars and pheromones production that attracts insects. New climatic conditions may alter leaf palatability or deadwood accumulation, compromising insect attraction	Backhaus et al. (2014), Bolte et al. (2010), Caldeira et al. (2002), Castagneyrol et al. (2018), Haavik et al. (2015), Hale et al. (2005), Hart et al. (2014a, b), Hogg et al. (2002), Itter et al. (2019), Kelsey et al. (2014), Kelsey and Joseph (2001), Klutsch et al. (2017) and Ward et al. (2019)
	Tree susceptibility to insect	Drought weakens the defensive system of trees (e.g. resins and other metabolites, water potential) and reduced capacity of fixing nitrogen which contributes to insect pest establishment	Anderegg et al. (2015), Arango-Velez et al. (2014), Birch et al. (2019), Björkman (2000), Croise and Lieutier (1993), Dunn and Lorio (1993), Durand-Gillmann et al. (2014), Flake and Weisberg (2019), Flower et al. (2014), Gaylord et al. (2013), Jaime et al. (2019), Larsson and Björkman (1993), Lucash et al. (2018), McNulty and Boggs (2010), Moise et al. (2019), Negron et al. (2009), Pohl et al. (2006), Sangüesa-Barreda et al. (2015), Scheller et al. (2018), Suárez-Vidal et al. (2019), Temperli et al. (2015), Wermelinger et al. (2008) and Wong and Daniels (2017)
	Tree susceptibility to drought	Insect pest attacks compromise tree response to later drought disturbances	Altmann (2013), Bouzidi et al. (2019), Cailleret et al. (2017), DeRose and Long (2012), Itter et al. (2019) and Lloret and Kitzberger (2018)
	Forest structure and composition	Drought modifies forest structure and composition, directly kills trees and following insects cannot establish	Hart, Veblen, et al. (2015)
Diseases or other pests	Attraction to the tree	A first pest disturbance causes tree stress leading to an increase of ethanol, monoterpenes and pheromones production, which attracts a second pest disturbance	Aukema et al. (2006), Beh et al. (2014), Gehring et al. (2013), Grégoire et al. (2015), Kelsey and Manter (2004), Kenaley et al. (2008) and Martini et al. (2017)
	Insect vector and symbiosis	Insects and other pest have a direct or indirect symbiotic collaborative relationship that includes insects acting as vectors for other forest diseases, promoting their spread and establishment	Addison et al. (2014), Aukema et al. (2010), Ceriani-Nakamurakare et al. (2016), Firmino et al. (2017), Pinna et al. (2019), Rankin and Borden (1991), Reed et al. (2015), Shanahan et al. (2016) and Xu et al. (2018)
	Interspecific competition	Insects compete for space, resources, or protect trees from second infestations	Borkowski and Skrzecz (2016), Bylund and Tenow (1994), Jones et al. (2015), Kennedy and McCullough (2002), Kopper et al. (2004), Maňák et al. (2013), (2015), Rankin and Borden (1991), Tabacaru and Erbilgin (2015) and Tabacaru et al. (2015)
Management	Forest consequences	Landscape pattern changes due the interaction of insect pests and forest management	Fettig et al. (2008) and Mladenoff et al. (2000)
	Attraction to the tree	Management causes tree stress leading to an increase of monoterpenes production what attracts insects	Bauce and Fuentealba (2013) and Leverkus et al. (2018)
	Forest structure and composition	Forest management reduces insect pest attacks by changing tree species, structure, and density	(Zhang et al. (1993), Anhold et al. (1996), Ager et al. (2007), Johansson et al. (2007), Hayes et al. (2008), Berthiaume et al. (2009), Fettig et al. (2010), Gustafson et al. (2010), Rossi et al. (2011), 2018), Schwab et al. (2011), D'Amato et al. (2011), James et al. (2011), Temperli et al. (2014), Nowak et al. (2015), Rosenberger et al. (2017), Leite et al. (2018), Cotton-Gagnon et al. (2018) and Restaino et al. (2019))

Table 2 continued

Perturbation	Interaction cause	Ecological explanation	References
Pollution and acid rain	Tree susceptibility to insects	Host tree fitness affected by high CO_2, O_3, other pollutants, or acid rain may consequently alter later insect attacks	Agrell et al. (2005), Awmack et al. (2004), Coviella and Trumble (1999), Docherty et al. (1997), Holopainen et al. (1993), Holton et al. (2003), Kidd (1990), Kinney et al. (1997), Kozlov et al. (2017), Lindroth et al. (1993), McDonald et al. (1999), Roth et al. (1998), Roth and Lindroth (1994) and Williams et al. (1994)
	Natural enemies	Pollution demonstrate a disrupted synchrony between natural enemies and insects	Saikkonen and Neuvonen (1993)
Other disturbances	Forest structure and composition	Disturbances causes changes in forest structure and composition, compromising later insect attacks	Hanewinkel et al. (2008), Radl et al. (2017), Tabacaru et al. (2016) and Thom et al. (2013)
	Tree susceptibility to insects	Disturbances such snow, storms, wind, or floods weakens the defensive system of trees (e.g. resins and other metabolites) contributing to insect pests establishment	Angulo-Sandoval et al. (2004), Howe and Baker (2003), Hunter and Forkner (1999), Reyes and Kneeshaw (2008) and Yoneya et al. (2014)
	Insect dispersion	Wind favors insect dispersion	Havašová et al. (2017) and Potterf and Bone (2017)
	Tree susceptibility to other disturbances	Insect pest compromises tree root systems exposing them to more susceptibility to debris slides	Simard and Lajeunesse (2015)

insect outbreaks and fire, arguing that insect attacks reduce forest fuel connectivity and therefore fire activity (DeRose and Long 2009). Still other studies have suggested that the varying responses of fire ignition to insect activity is due to the different temporal scales at which researchers have looked for these interactions: when examining the effect of spruce budworm (*C. fumiferana*) outbreaks on fire ignition risk in Ontario (Canada), James et al. (2017) found that immediately following an outbreak the risk decreased but, 9 to 10 years after the outbreak, ignition risk increased. However, at broad spatiotemporal scales, studies found that other factors such as climate, forest structure, and topography had a greater influence on fire ignition risk than did the spatial legacies of past insect outbreaks (Andrus et al. 2016; Speer and Kulakowski 2017). The specific ecology of the insect species of interest (Meigs et al. 2015; Cohen et al. 2016), severity of the outbreak (Simard et al. 2011; Meigs et al. 2015, 2016), and eco-regional context (James et al. 2017) also affect fire–insect relationships.

Fires also shape the probability of insect outbreaks, directly through their effects on tree resistance and indirectly through their effects on forest structure and succession. Interactions between fire and insects affect successional trajectories by reducing regeneration potential (Veblen et al. 2006). Alternatively, the compounded effects of fire and insects also facilitate regeneration by reducing tree competition, favoring seed dispersal (Land and Rieske 2006; Liang et al. 2016), changing forest-age structure (Arbellay et al. 2017), and replacing dominant species (Bergeron et al. 1993). A study on the spruce budworm (*C. fumiferana*) system suggests no effect of fire–insect interactions on long-term forest composition due to rapid regeneration of its primary host (Sturtevant et al. 2012).

In terms of direct effects, non-stand-replacing fires compromise tree defenses, making them more susceptible to insect attacks, due to both a reduction in bark thickness and to stress, which reduces resin production (Ryan and Amman 1996; Bradley and Tueller 2001; Santoro et al. 2001; Lombardero and Ayres 2011; Davis et al. 2012; Boulanger et al. 2013). Fire-injured trees also synthesize and accumulate ethanol, monoterpenes, and hormones that, once released to the atmosphere, act as primary attractant for some insect species such as *Dendroctonus valens*, *D. brevicomis, Gnathotrichus pilosus*, or *Hylurgops porosus* (Kelsey and Joseph 2003; Beh et al. 2014; Kelsey and Westlind 2017a; Westlind and Kelsey 2019), which can promote outbreaks.

Drought: insect pests

Much like fire-stress, drought influences insect-pest outbreaks because drought-stressed trees synthesize chemicals that act as insect attractants and, at the same time, may reduce their leaf- and stem-water potential limiting their resistance to insect attacks (Kelsey and Joseph 2001; Lusebrink et al. 2011; Kelsey et al. 2014; Anderegg et al. 2015; Klutsch et al. 2017). In the case of defoliators, drought stress can increase tree vulnerability as trees produce fewer palatable leaves and therefore insects need to consume more foliage to survive (Backhaus et al. 2014). Stressed trees are also limited in their ability to capture nutrients (McNulty and Boggs 2010) and produce resins, which makes them less able to defend themselves against insect attacks and therefore more vulnerable (Sangüesa-Barreda et al. 2015; Wong and Daniels 2017).

Conversely, insect outbreaks increase tree vulnerability to water stress. When trees are attacked by insects the crown and/or roots are damaged, compromising water-regulation capacity. Thus, trees become more susceptible to later episodes of extreme drought leading to higher mortality rates (McDowell et al. 2008, 2010; Allen et al. 2010; DeRose and Long 2012; Altmann 2013; Anderegg et al. 2015; Kolb et al. 2016). Some authors have down-played the relevance of drought–insect interactions arguing that such interactions are secondary relative to other factors, such as tree fitness or the consequences of forest management (Hart et al. 2015a, b). Indeed, some studies have proposed that water stress reduces trees' vulnerability to insect attack because of the less hospitable environment insects experience in a drought-stressed tree (Hart et al. 2014a, b; Kolb et al. 2016). Yet other studies have provided evidence that defoliators can enhance tree water status by reducing canopy transpiration under drought, which is called the defoliation paradox (Bouzidi et al. 2019; Itter et al. 2019).

Diseases or other insect pests: insect pests

Insect pests also interact with other biotic disturbances, such as diseases, pathogens, and other insects. These interactions may take the form of mutualisms, such as in the case where insects act as vectors for fungal infections such as Dutch elm disease or beech bark disease (the first caused by fungus *Ophiostoma ulmi* and the second by *Neonectria faginata* and *N. ditissima;* Rankin and Borden 1991; Aukema et al. 2010; Addison et al. 2014; Reed et al. 2015; Ceriani-Nakamurakare et al. 2016; Shanahan et al. 2016; Firmino et al. 2017; Xu et al. 2018; Pinna et al. 2019) or vectors for other bark beetle species (Croise and Lieutier 1993). As happens in the cases of fire and drought, when insects or fungi attack trees, they induce the production of volatile chemicals that attract other insects (Kelsey and Manter 2004; Aukema et al. 2006; Grégoire et al. 2015; Martini et al. 2017). However, inter-specific competition among insects or pathogens may diminish effects on host trees (Rankin and Borden 1991; Kennedy and McCullough 2002; Kopper et al. 2004; Tabacaru and Erbilgin 2015).

Forest management: insect pests

Pest control through forest management is a major topic that is out of the scope of this review. However, forest management (whether focused on pest control or not) causes alterations to forest landscapes and may interact with insect pest disturbances. Forest management affects insect outbreaks both negatively and positively (Fig. 3) and at different scales, from individual trees to landscapes (Hindmarch and Reid 2001; Ager et al. 2007; Johansson et al. 2007; Temperli et al. 2014). Thinning, prescribed burning, and commercial plantations change forest composition, landscape mosaics, and tree-age distributions. The "silvicultural hypothesis" states that forest diversity can mitigate the effects of outbreaking insects (Miller and Rusnock 1993; Jactel and Brockerhoff 2007). This hypothesis is supported by repeated observations that more diverse forest stands comprising hardwood species tend to experience less damage than homogenous coniferous stands do (Su et al. 1996; Campbell et al. 2008). Further, in a recent long-term study, Robert et al. (2018) found that the legacy of forest management strategies helped to explain the frequency, intensity, and spatial synchrony of spruce budworm (*C. fumiferana*) outbreaks. Removing dead trees, replanting new tree species, or prescribed burns interfered with outbreak development and spread (D'Amato et al. 2011; Rossi et al. 2011). Also, thinned stands were less susceptible to bark beetle species attack, likely because the plumes of pheromone the insects use for communication could not reach their targets (Thistle 2005), and because vigor and resistance to insect attacks was improved in thinned trees (Anhold et al. 1996; Macquarrie and Cooke 2011).

Pollution: insect pests

Pollution also interacts with insect pest disturbances. Most research indicates that pollutants reduce host-tree quality as well as insect fitness, leading to a reduction in insect attacks. For instance, high ozone concentrations reduce insect fecundity and colonization rates. Increased CO_2 and heavy metal concentrations reduce growth, survival, development, and size of larvae and adults (Kopper and Lindroth 2003). Acid rain negatively affects insects directly by causing mortality, or indirectly by reducing host-plant quality (Kinney et al. 1997; Butler and Trumble 2008). However, some studies find little influence of pollution on insect performance or even a positive influence (Awmack et al. 2004). Some aphids and lepidopterans increase their growth rate and survival under high concentration of SO_2, NO_2, or O_3 (Butler and Trumble 2008). Elevated concentrations of CO_2 may play a role in insect interactions with pathogens (Roth and Lindroth 1994; Roth et al. 1998; Stiling et al. 1999) or insects' natural enemies (Percy et al. 2002), although most common responses were negative or neutral. Some studies verified that under simulated acid rain conditions, insect attacks were more severe than in the control situation (Palokangas and Neuvonen 1995; Saikkonen et al. 1995).

Other disturbances: insect pests

Other disturbances such as storms, windthrow, snow avalanches, and landslides influence insect outbreaks and their effects on forests. Together, these agents build a complex picture of direct, indirect, bidirectional, and multidirectional interactions. Such disturbances may cause changes in forest structure, compromising later insect attacks (Hanewinkel et al. 2008; Louis et al. 2014; Perovich and Sibold 2016). Also, after severe gales, storms, or landslides, the accumulation of dead wood and hence the probability of insect attacks may increase (Howe and Baker 2003; Yamazaki 2011; Simard and Lajeunesse 2015). Finally, some authors have mentioned that episodes of strong winds might facilitate the spread of insect pests (Stadelmann et al. 2014; Havašová et al. 2017; Potterf and Bone 2017).

Climate change: insect pests

Climate change is not a forest disturbance in itself, but it has been widely recognized as a major driver of changes in insect pest regimes (Rouault et al. 2006; Bolte et al. 2010; DeRose and Long 2012; Temperli et al. 2013, 2015; Pawson et al. 2017; Rogers et al. 2017). Like many of the disturbances we have discussed, climate change influences insect pests both directly and indirectly. In terms of direct effects, increases in temperature and changes in moisture availability may increase insect survival and development rates (van Lierop et al. 2015; Malesky et al. 2018). These changes are likely to lead to shifts in geographic distributions (Friedenberg et al. 2008; Bolte et al. 2010; DeRose and Long 2012; Schwartzberg et al. 2014; Renwick et al. 2016; Marini et al. 2017; Pawson et al. 2017; Rogers et al. 2017; Jaime et al. 2019), although such positive feedback is still under discussion (Pyšek et al. 2010). In terms of indirect effects, climate change affects insect pests through direct and indirect influence on other agents (Pechony and Shindell 2010; Temperli et al. 2013; Seidl and Rammer 2017; Seidl et al. 2017).

Sources of variation in disturbance interactions

The interactions between insect pests and other forest disturbances highlighted in this review were often significant and synergistic (Fig. 3). Disturbances disrupt the structure and composition of ecosystems, create heterogeneous landscape mosaics, and change the physical environment (White and Pickett 1985; Turner 2010). In doing so, they can force ecosystem renewal, cause temporal disorganization, and alter the susceptibility of forests to new disturbances. Such synergistic interactions are especially important for the dynamics of biotic disturbances in a changing climate (Seidl et al. 2017).

In this review, we aimed to identify the main elements that favor or limit forest disturbance interactions. Different authors emphasize the relevance of the particular insect species involved in the interaction (Joseph et al. 2001; Hanula et al. 2002; Meigs et al. 2015, 2016; Kelsey and Westlind 2017a), as different species tend to have different autecologies and vary in terms of feeding strategies, even within feeding guilds. Further, some species were studied more than others with respect to their interactions with other disturbances (e.g., the interactions between *Dendroctonus* spp. and *C. fumiferana* with fire). We therefore hypothesized that insect feeding guild (i.e., defoliators vs. xylem/phloem feeders) might be associated with particular disturbances, but the results presented here did not support this theory. Only disturbances caused by xylem/phloem feeders tended to occur more frequently following periods of drought, probably due to the higher concentration of soluble sugars in the bark of water-stressed trees resulting in improved insect larvae performance (Caldeira et al. 2002).

We hypothesized that interactions between disturbances might be more frequent at smaller spatial (at the physiological- and tree-scale) and temporal scales (1 year or less; Fig. 4). When larger spatiotemporal scales are considered, there may be more agents and processes that influence forest dynamics and disturbance and, therefore, it becomes more difficult to identify clear relationships between disturbances. Also, interactions at small spatiotemporal scales, such as positive attraction of insects at the physiological scale a few days after a fire or drought, are probably unlikely to translate into landscape-scale outbreaks (Kelsey and Joseph 2001, 2003; Kelsey et al. 2016; Kelsey and Westlind 2017a, b). However, although we identified differences in the frequency of interactions according to spatial and temporal scale, these were not significant. Thus, we concluded that scales are not correlated with the probability of identifying an interaction between two disturbances.

Studies of interactions between disturbances include a broad range of disturbance-specific features (e.g., fire disturbances are described with respect to size, severity, probability of ignition) that may affect the interaction. This is the case that Meigs (2015, 2016) and Harvey (2013, 2014) presented when they reported that insect attacks did not increase fire likelihood but altered its severity and spread. Thus, in this study we specified the type of response in disturbance interactions reported in every study (influences on the likelihood, severity, spread or insect fitness). Most of the reviewed papers that focused on insect–fire interactions examined how increased fuel loads caused by insect attacks (according to the duration of defoliation and time since the end of defoliation) facilitate subsequent fire ignition (e.g., Watt et al. 2020). In respect of severity, studies such as Derose and Long (2009) and Donato et al. (2013) reported a reduction in fire severity following insect attack because defoliation resulted in reduced horizontal and vertical fuel connectivity. However, our results showed that the occurrence of interactions between disturbances was not correlated with the type of response considered, either for the specific case of fire or for other disturbances. Only a small relationship between pollution and its impacts on insect fitness was found. Thus, we highlight the importance of characterizing the specific nature of disturbance interactions and the consequences on disturbed ecosystems, in addition to identifying when and where an interaction occurs.

The role of simulation models

There is increasing interest in examining the combined effects of multiple disturbances on landscape dynamics (Chew et al. 2004; Temperli et al. 2015; Seidl et al. 2016; Tabacaru et al. 2016; Lucash et al. 2018; Scheller et al. 2018). However, empirical approaches are limited in their ability to address such complex questions because past disturbances may provide an insufficient basis to understand potential future changes resulting from climate change, invasive species, and increasing human activity (Temperli et al. 2013, 2015). Simulation modeling provides one useful approach to studying future landscape changes and exploring emergent dynamics (Perera 2015).

Nonlinear, cross-scale interactions are inherent in forest landscape dynamics (e.g., interactions at tree level may leave a footprint at the landscape level; Peters et al. 2007). Empirical approaches have limited application at broad temporal and spatial scales or when processes occur across scales. Most of the modeling studies we reviewed used spatially explicit models at the scale of the landscape or stand. These models also explored longer time frames than did empirical studies (Fig. 5), of up to 300 years (James et al. 2011a; Hoffman et al. 2012a, b; Sturtevant et al. 2012; Loehman et al. 2017). The ability to explore long-term dynamics is essential in the case of insect pest disturbances because of the long term spatial legacies they can create and, in some cases, the cyclical population dynamics they generate (Fig. 5; Robert et al. 2020).

Future environmental change is uncertain, as are the dynamics of stochastic disturbances. Simulation models allows for the explicit integration of this uncertainty through scenario testing. Model-mediated exploration of such uncertain parameter space is essential to improve understanding of how different sources of uncertainty might impact the target system. Most of the articles we examined here engaged in some sort of scenario testing. (Fig. 5). Scenarios were mainly used to analyze the role of climate change in forest disturbances, usually using the IPCC climate projections (Moss et al. 2010). Other studies used scenarios to test different disturbance impacts or the response of the affected habitat (Fig. 5). Long-term projections based on a range of plausible scenarios are also valuable in facilitating policy development (Økland et al. 2016; Morán-Ordóñez et al. 2018).

While a modeling approach has benefits relative to relying on historical empirical data (e.g., the opportunity to observe unexpected emergent phenomena), developing spatial models of forest disturbance interactions can be challenging. A central challenge relates to the acquisition of high-quality data for parameterizing complex spatially-explicit simulation models, especially at large scales. Indeed, the lack of such information often stimulates the adoption of a modeling approach. Some authors collected their own data to calibrate the model DeRose and Long 2009; Simard et al. 2011; Hoffman et al. 2012a, b; Nitschke et al. 2012; Linn et al. 2013; Hansen et al. 2015; Økland et al. 2016), whereas others used another approach, simulating the input data of the model based on expert knowledge (Temperli et al. 2015). Most modeling studies we reviewed here used data from public repositories or from other publications (Fig. 5). Long-term data monitoring and remote sensing data are particularly useful in landscape dynamics modeling because these sources offer continuous information in time and/or space (Chapin and Starfield 1997; Ager et al. 2007; Gustafson et al. 2010).

Other challenges to developing useful models of forest disturbance include integrating multiple relevant processes and their interactions at different spatiotemporal scales, as well as modeling them in a mechanistic way (Baker and Robinson 2010). Addressing these challenges requires explicit assumptions and simplifications, compromising realism while maintaining coherence, internal consistency, and plausible descriptions of modelled dynamics (Baker and Robinson 2010; Morán-Ordóñez et al. 2018). Thus, when working with multiple disturbances, one is restricted to including only relevant landscape variables (one or a few in number) both as explanatory and response variables (e.g., stand volume, species; Clark and Gelfand 2006; Gustafson et al. 2010).

Of the 216 articles we reviewed, only 23 were based on simulation models. However, interest in using simulation modeling to explore disturbance interactions seems to be increasing: 83% of the model-based studies were published after 2010. Given the utility of simulation models mentioned above, both in scientific research and in the development of forest policies, we would emphasize the importance of the further development of simulation modeling capacity through research on how to better model complex processes and their multi-scale dynamics. To complement such model development, additional empirical information is required to improve model parameterization and model predictions, and it is the reciprocal interaction between empirical and simulation studies that will identify new challenges and opportunities and move our collective understanding forward.

Emerging disturbances and challenges to their study

Climate change, increasing global trade, and land-use change all have the potential to alter interactions between insect pests and other disturbances. Such drivers lead to an increase in invasive species that will compromise host ecosystems (Brockerhoff et al. 2006; Lovett et al. 2006; Ward and Masters 2007; Smith et al. 2012; Dix and Britton 2014; van Lierop et al. 2015; Choi et al. 2019). Some species considered to be invasive were introduced centuries ago and their effects on ecosystems are usually considered alongside native species. That is the case with the gypsy moth (*L. dispar*), which is of Euro Asiatic origin but was introduced to the US at the end of the nineteenth century (Kinney et al. 1997; Roth et al. 1998; McDonald et al. 1999). However, impacts of recent invasive insect pests are hard to predict because there is little empirical evidence about their performance in new environments with new competitors. One such species is the box tree moth (*Cydalima perspectalis*) native to Asia, which has been invading European forests since 2007 (Bras et al. 2019). Its defoliating effect leads to the death of box trees (*Buxus* *sempervirens*), which are abundant in the understories of European forests. This may cause an increase in fuel availability and consequently affect the severity of fire risk or, conversely, it may reduce the probability of fire spread by eliminating the main understory species and reducing fuel connectivity.

Land-use change poses another challenge to understanding interactions between insects and other forest disturbances. It is broadly assumed that the replacement of primary forests with pastures and croplands causes a reduction in insect biodiversity, as seen in different ecosystems around the world (Koh 2007; Almeida et al. 2011; Meijer et al. 2011; Korasaki et al. 2013). Moreover, Barragán et al. (2011) documented a loss in beetle functional diversity (based on food relocation, body size, daily activity period, and food preferences) as a result of land-use changes in Mexico. However, the study of land-use effects on insect pests is mainly focused on agriculture (Kiritani 2007; van Lierop et al. 2015), and few studies investigate forest insects in the context of land-use change (Rosenberger et al. 2017). An example may be the pine processionary moth (*Thaumetopoea pityocampa*), whose growth is linked to habitat type (Torres-Muros et al. 2017). Given rural abandonment and pine reforestation in the natural range of this insect species (Pausas et al. 2008; Cervera et al. 2019), an increase in pine processionary moth pest risk is possible. Thus, researchers and managers should acknowledge that current dynamics and management policy effects extend beyond the short-term and local scale and should pay special attention not only to current forest pests but also to those that may have future impacts (Table 2).

Finally, it is essential to improve theoretical knowledge of outbreaking insect species (genetics, population dynamics, species ecology, and distribution) to better understand the mechanisms behind interaction dynamics (Ayres and Lombardero 2000; Loehman et al. 2017; Xu et al. 2018). Other authors have highlighted problems with obtaining high-quality data for such studies, because long-term and broad-scale monitoring is needed (Hanula et al. 2002; Aukema et al. 2010; Gustafson et al. 2010). New technologies and platforms, such as data obtained using satellites or LiDAR, as well as improved demographic and population genetic data, represent enormous resources with which we can better parameterize spatially-explicit simulation models (Chou et al. 2010; Hollaus and Vreugdenhil 2019).

Conclusions

Our review summarizes the current understanding of interactions between insect pest outbreaks and other forest disturbances and highlights the complexity of these processes. Such interactions are critical drivers of landscape dynamics in many forested systems. Reported interactions between disturbances were synergistic, antagonistic, or not detected. They were detected at different spatial (from tree to landscape level) and temporal (from days to century) scales and included various types of interaction (influences on the likelihood, severity, spread or insect fitness). However, we found no clear relation between such disturbance features and the occurrence of interactions.

The impacts of insect pest outbreaks are expected to increase with intensifying global change. The fitness and distribution of insect species are strongly influenced by climate. Furthermore, insect pest outbreaks can interact with pollution and land-use changes, and invasions by insect species are increasing as a result of global trade. Understanding the potential for altered interactions between insect pests and other disturbances as well as the emergence of novel interactions are major challenges in forest dynamics research. In this context, simulation models and spatially explicit simulations of potential future global-change scenarios may play an important role in the management of disturbance interactions and landscape dynamics because they can incorporate multiple drivers that operate at broad spatiotemporal scales and can be used to project possible future scenarios. Such predictions of future ecosystem conditions must be supported by appropriate theoretical knowledge and must be relevant to decision-making processes.

Acknowledgements This study was motivated, and ideas shaped thorough several inspirational talks with Garrett Meigs, Meg Krawchuk, David Shaw, Gabriela Ritokova, Rick G. Kelsey, Henry Lee, David Bell and Matthew Reilly that we deeply thank. This study was funded by the Spanish Government through the INMODES (CGL2017-89999-C2-2-R) and the European Union's H2020 Research and Innovation Program under the Marie Sklodowska-Curie Grant Agreement No. 691149 (SuFoRun). A proofreading of the manuscript was completed by Proof Reading Service.

Author contribution All authors contributed to the study. Idea for the article was originated by CQ, BL and JPMA. Study conception and design was realized by CQ and BL Literature search and data analysis was performed by CQ. The first draft of the document was written by CQ and all authors (CQ, AN, LJJ, JPMA, BL) commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability All data generated or analysed during this study are included in this published article and its Supplementary Information files.

References

Addison A, Powell JA, Bentz BJ, Six DL (2014) Integrating models to investigate critical phenological overlaps in complex ecological interactions: the mountain pine beetle-fungus symbiosis. J Theor Biol 368:55–66

Ager AA, McMahan A, Hayes JL, Smith EL (2007) Modeling the effects of thinning on bark beetle impacts and wildfire potential in the Blue Mountains of eastern Oregon. Landsc Urban Plan 80:301–311

Agne MC, Beedlow PA, Shaw DC, Woodruff DR, Lee EH, Cline SP, Comeleo RL (2018) Interactions of predominant insects and diseases with climate change in Douglas-fir forests of western Oregon and Washington, U.S.A. For Ecol Manag 409:317–332

Agne MC, Woolley T, Fitzgerald S (2016) Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. For Ecol Manag 366:73–86

Agrell J, Kopper B, McDonald EP, Lindroth RL (2005) CO_2 and O_3 effects on host plant preferences of the forest tent caterpillar (*Malacosoma disstria*). Glob Change Biol 11:588–599

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH (Ted.), Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684

Almeida S, Louzada J, Sperber C, Barlow J (2011) Subtle land-use change and tropical biodiversity: dung beetle communities in Cerrado grasslands and exotic pastures. Biotropica 43:704–710

Altmann SH (2013) Crown condition, water availability, insect damage and landscape features: are they important to the Chilean tree *Nothofagus glauca* (Nothofagaceae) in the context of climate change? Aust J Bot 61:394–403

Amman GD, Ryan KC (1991) Insect infestation of fire-injured trees in the Greater Yellowstone Area. USDA Forest Service, Intermountain Forest and Range Experiment Station

Anderegg WRL, Allen CD, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady K, Mcdowell N, Pan Y, Raffa K, Sala A (2015) Tree mortality from drought, insects, and their interactions in a changing climate. N Phytol 208:674–683

Andrus RA, Veblen TT, Harvey BJ, Hart SJ (2016) Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. Ecol Appl 26:700–711

Angulo-Sandoval P, Fernández-Marín H, Zimmerman JK, Aide TM (2004) Changes in patterns of understory leaf phenology and herbivory following hurricane damage. Biotropica 36:60

Anhold JA, Jenkins MJ, Long JN (1996) Management of lodgepole pine stand density to reduce susceptibility to mountain pine beetle attack. West J Appl For 11:50–53

Arango-Velez A, Galindo González LM, Meents MJ, El Kayal W, Cooke BJ, Linsky J, Lusebrink I, Cooke JEK (2014) Influence of water deficit on the molecular responses of *Pinus contorta* ×*Pinus banksiana* mature trees to infection by the mountain pine beetle fungal associate, *Grosmannia clavigera*. Tree Physiol 34:1220–1239

Arbellay E, Daniels LD, Mansfield SD, Chang AS (2017) Cambial injury in lodgepole pine (*Pinus contorta*): mountain pine beetle vs fire. Tree Physiol 37:1611–1621

Aukema BH, Richards GR, Krauth SJ, Raffa KF (2006) Species assemblage arriving at and emerging from trees colonized by *Ips pini* in the Great Lakes Region: partitioning by time since colonization, season, and host species. Ann Entomol Soc Am 97:117–129

Aukema BH, Zhu J, Møller J, Rasmussen JG, Raffa KF (2010) Predisposition to bark beetle attack by root herbivores and associated pathogens: roles in forest decline, gap formation, and persistence of endemic bark beetle populations. For Ecol Manag 259:374–382

Awmack CS, Harrington R, Lindroth RL (2004) Aphid individual performance may not predict population responses to elevated CO_2 or O_3. Glob Change Biol 10:1414–1423

Ayres MP, Lombardero M (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ. https://doi.org/10.1016/S0048-9697(00)00528-3

Backhaus S, Wiehl D, Beierkuhnlein C, Jentsch A, Wellstein C (2014) Warming and drought do not influence the palatability of *Quercus pubescens* Willd. leaves of four European provenances. Arthropod Plant Interact 8:329–337

Bakaj F, Mietkiewicz N, Veblen TT, Kulakowski D (2016) The relative importance of tree and stand properties in susceptibility to spruce beetle outbreak in the mid-20th century. Ecosphere 7:1–17

Baker PJ, Robinson A (2010) Review and comparison of tree- and stand-based forest growth models for potential integration into EnSym. University of Melbourne, Melbourne

Barbet-Massin M, Rome Q, Villemant C, Courchamp F (2018) Can species distribution models really predict the expansion of invasive species? PLoS ONE 13:1–14

Barragán F, Moreno CE, Escobar F, Halffter G, Navarrete D (2011) Negative impacts of human land use on dung beetle functional diversity. PLoS ONE. https://doi.org/10.1371/journal.pone.0017976

Bauce É, Fuentealba A (2013) Interactions between stand thinning, site quality and host tree species on spruce budworm biological performance and host tree resistance over a 6 year period after thinning. For Ecol Manag 304:212–223

Bebi P, Kulakowski D, Veblen TT (2003) Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology 84:362–371

Beh MM, Metz MR, Seybold SJ, Rizzo DM (2014) The novel interaction between *Phytophthora ramorum* and wildfire elicits elevated ambrosia beetle landing rates on tanoak, *Notholithocarpus densiflorus*. For Ecol Manag 318:21–33

Bergeron Y, Pierre-Rene D, Dansereau PRP-R (1993) Predicting the composition of Canadian southern boreal forest in different fire cycles. J Veg Sci 4:827–832

Berthiaume R, Bauce É, Hébert C, Brodeur J (2009) Host tree age as a selective pressure leading to local adaptation of a population of a polyphagous Lepidoptera in virgin boreal forest. Bull Entomol Res 99:493–501

Bigler C, Kulakowski D, Veblen TT (2005) Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology 86:3018–3029

Birch JD, Lutz JA, Hogg EH, Simard SW, Pelletier R, LaRoi GH, Karst J (2019) Decline of an ecotone forest: 50 years of demography in the southern boreal forest. Ecosphere. https://doi.org/10.1002/ecs2.2698

Björkman C (2000) Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. Oecologia 123:223–231

Bolte A, Hilbrig L, Grundmann B, Kampf F, Brunet J, Roloff A (2010) Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce-beech forest. Eur J For Res 129:261–276

Borkowski A, Skrzecz I (2016) Ecological segregation of bark beetle (Coleopter Curculionida Scolytinae) infested Scots pine. Ecol Res 31:135–144

Boucher D, Boulanger Y, Aubin I, Bernier PY, Beaudoin A, Guindon L, Gauthier S (2018) Current and projected cumulative impacts of fire, drought, and insects on timber volumes across Canada. Ecol Appl 28:1245–1259

Boulanger Y, Sirois L, Hébert C (2013) Distribution patterns of three long-horned beetles (Coleoptera: Cerambycidae) shortly after fire in boreal forest: adults colonizing stands versus progeny emerging from trees. Environ Entomol 42:17–28

Bouzidi HA, Balducci L, Mackay J, Deslauriers A (2019) Interactive effects of defoliation and water deficit on growth, water status, and mortality of black spruce (*Picea mariana* (Mill.) B.S.P.). Ann For Sci. https://doi.org/10.1007/s13595-019-0809-z

Bradley T, Tueller P (2001) Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe basin. For Ecol Manag 142:205–214

Bras A, Avtzis DN, Kenis M, Li H, Vétek G, Bernard A, Courtin C, Rousselet J, Roques A, Auger-Rozenberg MA (2004) (2019) A complex invasion story underlies the fast spread of the invasive box tree moth (*Cydalima perspectalis*) across Europe. J Pest Sci 92:1187–1202

Brockerhoff EG, Liebhold AM, Jactel H (2006) The ecology of forest insect invasions and advances in their management. Can J For Res 36:263–268

Buma B, Wessman CA (2011) Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2:1–13

Burton PJ, Boulanger Y (2018) Characterizing combined fire and insect outbreak disturbance regimes in British Columbia, Canada. Landsc Ecol 33:1997–2011

Butler CD, Trumble JT (2008) Effects of pollutants on bottom-up and top-down processes in insect–plant interactions. Environ Pollut 156:1–10

Bylund H, Tenow O (1994) Long-term dynamics of leaf miners, *Eriocrania* spp., on mountain birch: alternate year fluctuations and interaction with *Epirrita autumnata*. Ecol Entomol 19:310–318

Cailleret M, Jansen S, Robert EMR, Desoto L, Aakala T, Antos JA, Beikircher B, Bigler C, Bugmann H, Caccianiga M, Čada V, Camarero JJ, Cherubini P, Cochard H, Coyea MR, Čufar K, Das AJ, Davi H, Delzon S, Dorman M, Gea-Izquierdo G, Gillner S, Haavik LJ, Hartmann H, Hereş AM, Hultine KR, Janda P, Kane JM, Kharuk VI, Kitzberger T, Klein T, Kramer K, Lens F, Levanic T, Linares Calderon JC, Lloret F, Lobo-Do-Vale R, Lombardi F, López Rodríguez R, Mäkinen H, Mayr S, Mészáros I, Metsaranta JM, Minunno F, Oberhuber W, Papadopoulos A, Peltoniemi M, Petritan AM, Rohner B, Sangüesa-Barreda G, Sarris D, Smith JM, Stan AB, Sterck F, Stojanović DB, Suarez ML, Svoboda M, Tognetti R, Torres-Ruiz JM, Trotsiuk V, Villalba R, Vodde F, Westwood AR, Wyckoff PH, Zafirov N, Martínez-Vilalta J (2017) A synthesis of radial growth patterns preceding tree mortality. Glob Change Biol 23:1675–1690

Caldeira M, Fernandéz C, Tomé V, Pereira J (2002) Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks. Ann For Sci 59:99–106

Campbell EM, MacLean DA, Bergeron Y (2008) The severity of budworm-caused growth reductions in balsam fir/spruce stands varies with the hardwood content of surrounding forest landscapes. For Sci 54:195–205

Candau JN, Fleming RA, Wang X (2018) Ecoregional patterns of spruce budworm–wildfire interactions in central Canada's Forests. Forests. https://doi.org/10.3390/f9030137

Carnegie AJ, Stone C, Lawson S, Matsuki M (2005) Can we grow certified eucalypt plantations in subtropical Australia? An insect pest management perspective. N Z J For Sci 35:223–245

Castagneyrol B, Moreira X, Jactel H (2018) Drought and plant neighbourhood interactively determine herbivore consumption and performance. Sci Rep 8:1–12

Ceriani-Nakamurakare E, Slodowicz M, Gonzalez-Audino P, Dolinko A, Carmarán C (2016) Mycobiota associated with the ambrosia beetle *Megaplatypus mutatus*: threat to poplar plantations. Forestry 89:191–200

Cervera T, Pino J, Marull J, Padró R, Tello E (2019) Understanding the long-term dynamics of forest transition: from deforestation to afforestation in a Mediterranean landscape (Catalonia, 1868–2005). Land Use Policy 80:318–331

Chang WY, Lantz VA, Hennigar CR, Maclean DA (2012) Economic impacts of forest pests: a case study of spruce budworm outbreaks and control in New Brunswick, Canada. Can J For Res 42:490–505

Chapin FS, Starfield AM (1997) Time lags and novel ecosystems in response to transient climatic change in Arctic Alaska. Clim Change 35:449–461

Chen G, He Y, De Santis A, Li G, Cobb R, Meentemeyer RK (2017) Assessing the impact of emerging forest disease on wildfire using Landsat and KOMPSAT-2 data. Remote Sens Environ 195:218–229

Chen-Charpentier B, Leite MCA (2014) A model for coupling fire and insect outbreak in forests. Ecol Model 286:26–36

Chew JD, Stalling C, Moeller K (2004) Integrating knowledge for simulating vegetation change at landscape scales. West J Appl For 19:102–108

Choi WI, Nam Y, Lee CY, Choi BK, Shin YJ, Lim JH, Koh SH, Park YS (2019) Changes in major insect pests of Pine forests in Korea over the last 50 years. Forests 10:1–15

Chou CY, Song B, Hedden RL, Williams TM, Culin JD, Post CJ (2010) Three-dimensional landscape visualizations: new technique towards wildfire and forest bark beetle management. Forests 1:82–97

Clark JS, Gelfand AE (2006) A future for models and data in environmental science. Trends Ecol Evol 21:375–380

Cohen WB, Yang Z, Stehman SV, Schroeder TA, Bell DM, Masek JG, Huang C, Meigs GW (2016) Forest disturbance across the conterminous United States from 1985–2012: the emerging dominance of forest decline. For Ecol Manag 360:242–252

Coleman TW, Meeker JR, Clarke SR, Rieske LK (2008) The suppression of *Dendroctonus frontalis* and subsequent wildfire have an impact on forest stand dynamics. Appl Veg Sci 11:231–242

Colgan LJ, Erbilgin N (2010) The ecological interaction of the mountain pine beetle and jack pine budworm in the boreal forest. For Chron 86:766–774

Cotton-Gagnon A, Simard M, De Grandpré L, Kneeshaw D (2018) Salvage logging during spruce budworm outbreaks increases defoliation of black spruce regeneration. For Ecol Manag 430:421–430

Coviella CE, Trumble JT (1999) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. Conserv Biol 13:700–712

Croise L, Lieutier F (1993) Effects of drought on the induced defence reaction of Scots pine to bark beetle-associated fungi. Ann des Sci For 50:91–97

Crotteau JS, Keyes CR, Hood SM, Affleck DLR, Sala A (2018) Fuel dynamics after a bark beetle outbreak impacts experimental fuel treatments. Fire Ecol 14:13

Cullingham CI, Cooke JEK, Dang S, Davis CS, Cooke BJ, Coltman DW (2011) Mountain pine beetle host-range expansion threatens the boreal forest. Mol Ecol 20:2157–2171

D'Amato AW, Troumbly SJ, Saunders MR, Puettmann KJ, Albers MA (2011) Growth and survival of *Picea glauca* following thinning of plantations affected by eastern Spruce budworm. North J Appl For 28:105–150

Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres M, Flannigan MD, Hanson PJ, Irland LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stoks BJ, Wotton M (2001) Climate change and forest disturbances. Bioscience 51:723

Davis RS, Hood S, Bentz BJ (2012) Fire-injured ponderosa pine provide a pulsed resource for bark beetles. Can J For Res 42:2022–2036

Day JK, Pérez DM (2013) Reducing uncertainty and risk through forest management planning in British Columbia. For Ecol Manag 300:117–124

DeRose RJ, Long JN (2009) Wildfire and spruce beetle outbreak: simulation of interacting disturbances in the central Rocky Mountains. Écoscience 16:28–38

DeRose RJ, Long JN (2012) Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. Can J For Res 42:1649–1660

Dix ME, Britton K (2014) A dynamic invasive species research vision: opportunities and priorities 2009-29. Invasive Species National Research Opportunities and Priorities and Strategic Management Framework, pp 1–222

Docherty M, Wade FA, Hurst DK, Whittaker JB, Lea PJ (1997) Responses of tree sap-feeding herbivores to elevated CO_2. Glob Change Biol 3:51–59

Donato DC, Harvey BJ, Romme WH, Simard M, Turner MG (2013) Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecol Appl 23:3–20

Duane A, Brotons L (2018) Synoptic weather conditions and changing fire regimes in a Mediterranean environment. Agric For Meteorol 253–254:190–202

Dunn JP, Lorio PL (1993) Modified water regimes affect photosynthesis, xylem water potential, cambial growth, and resistance of juvenile *Pinus taeda* L. to *Dendroctonus frontalis* (Coleoptera, Scolytidae). Environ Entomol 22:948–957

Durand-Gillmann M, Cailleret M, Boivin T, Nageleisen LM, Davi H (2014) Individual vulnerability factors of Silver fir (*Abies alba* Mill.) to parasitism by two contrasting biotic agents: Mistletoe (*Viscum album* L. ssp. *abietis*) and bark beetles (Coleoptera: Curculionidae: Scolytinae) during a decline process. Ann For Sci 71:659–673

Ehnström B, Långström B, Hellqvist C (1995) Insects in burned forests—forest protection and faunal conservation (preliminary results). Entomol Fenn 6:109–117

Elkin CM, Reid ML (2004) Attack and reproductive success of mountain pine beetles (Coleoptera: Scolytidae) in fire-damaged lodgepole pines. Environ Entomol 33:1070–1080

FAO (2008) Salud y vitalidad de los bosques. FAO, Rome, pp 69–88

Fettig C, Borys R, Dabney C (2010) Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. For Sci 56:60–73

Fettig CJ, Borys RR, McKelvey SR, Dabney CP (2008) Blacks Mountain Experimental Forest: bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. Can J For Res 38:924–935

Firmino PN, Calvao T, Ayres MP, Pimentel CS (2017) *Monochamus galloprovincialis* and *Bursaphelenchus xylophilus* life history in an area severely affected by pine wilt disease: implications for forest management. For Ecol Manag 389:105–115

Flake SW, Weisberg PJ (2019) Fine-scale stand structure mediates drought-induced tree mortality in pinyon–juniper woodlands. Ecol Appl 29:1–13

Fleming RA, Candau J-N, McAlpine RS (2002) Landscape-scale analysis of interactions between insect defoliation and forest fire in Central Canada. Clim Change 55:251–272

Flower A, Gavin DG, Heyerdahl EK, Parsons RA, Cohn GM (2014) Drought-triggered western spruce budworm outbreaks in the interior Pacific Northwest: a multi-century dendrochronological record. For Ecol Manag 324:16–27

Friedenberg NA, Sarkar S, Kouchoukos N, Billings RF, Ayres MP (2008) Temperature extremes, density dependence, and southern pine beetle (Coleoptera: Curculionidae) population dynamics in east Texas. Environ Entomol 37:650–659

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. N Phytol 198:567–578
Gehring CA, Cobb NS, Whitham TG (2013) The University of Chicago three-way interactions among ectomycorrhizal mutualists, scale insects, and resistant and susceptible pinyon pines reviewed work(s). Am Nat 149:824–841
Gitau CW, Bashford R, Carnegie AJ, Gurr GM (2013) A review of semiochemicals associated with bark beetle (Coleoptera: Curculionidae: Scolytinae) pests of coniferous trees: a focus on beetle interactions with other pests and their associates. For Ecol Manag 297:1–14
Gonzalez-Brambila CN, Reyes-Gonzalez L, Veloso F, Perez-Angón MA (2016) The scientific impact of developing nations. PLoS ONE. https://doi.org/10.1371/journal.pone.0151328
Graziosi I, Tembo M, Kuate J, Muchugi A (2020) Pests and diseases of trees in Africa: a growing continental emergency. Plants People Planet 2:14–28
Grégoire DM, Quiring DT, Royer L, Heard SB, Bauce É (2015) Indirect host-mediated effects of an exotic phloem-sap feeder on a native defoliator of balsam fir. For Ecol Manag 341:1–7
Gustafson EJ, Keene R (2014) Predicting changes in forest composition and dynamics—landscape-scale process models. US Department of Agriculture, Forest Service, Climate Change Resource Center
Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. Ecol Appl 20:700–715
Haavik LJ, Billings SA, Guldin JM, Stephen FM (2015) Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. For Ecol Manag 354:190–205
Hale BK, Herms DA, Hansen RC, Clausen TP, Arnold D (2005) Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. J Chem Ecol 31:2601–2620
Hanewinkel M, Breidenbach J, Neeff T, Kublin E (2008) Seventy-seven years of natural disturbances in a mountain forest area—the influence of storm, snow, and insect damage analysed with a long-term time series. Can J For Res 38:2249–2261
Hansen EM, Johnson MC, Bentz BJ, Vandygriff JC, Munson AS (2016) Forest-landscape structure mediates effects of a spruce bark beetle (*Dendroctonus rufipennis*) outbreak on subsequent likelihood of burning in Alaskan boreal forest. For Ecol Manag 369:38–46
Hansen EM, Johnson MC, Bentz BJ, James VC, Steven MA (2015) Fuel loads and simulated fire behavior in "old-stage" beetle-infested ponderosa pine of the Colorado Plateau. For Sci 61:644–664
Hanula JL, Meeker JR, Miller DR, Barnard EL (2002) Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. For Ecol Manag 170:233–247
Hart SJ, Schoennagel T, Veblen TT, Chapman TB (2015a) Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc Natl Acad Sci USA 112:4375–4380
Hart SJ, Veblen TT, Eisenhart KS, Jarvis D, Kulakowski D (2014) Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. Ecology 95:930–939
Hart SJ, Veblen TT, Kulakowski D (2014b) Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? For Ecol Manag 318:44–53
Hart SJ, Veblen TT, Mietkiewicz N, Kulakowski D (2015b) Negative feedbacks on bark beetle outbreaks: widespread and severe spruce beetle infestation restricts subsequent infestation. PLoS ONE 10:1–17
Harvey BJ, Donato DC, Romme WH, Turner MG (2013) Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. Ecology 94:2475–2486
Harvey BJ, Donato DC, Romme WH, Turner MG (2014) Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol Appl 24:1608–1625
Harvey BJ, Donato DC, Turner MG (2014) Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc Natl Acad Sci USA 111:15120–15125
Havašová M, Ferenčík J, Jakuš R (2017) Interactions between windthrow, bark beetles and forest management in the Tatra National Parks. For Ecol Manag 391:349–361
Hayes CJ, DeGomez TE, McMillin JD, Anhold JA, Hofstetter RW (2008) Factors influencing pine engraver (*Ips pini* Say) colonization of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) slash in Northern Arizona. For Ecol Manag 255:3541–3548
Hessburg PF, Churchill DJ, Larson AJ, Haugo RD, Miller C, Spies TA, North MP, Povak NA, Belote RT, Singleton PH, Gaines WL, Keane RE, Aplet GH, Stephens SL, Morgan P, Bisson PA, Rieman BE, Salter RB, Reeves GH (2015) Restoring fire-prone Inland Pacific landscapes: seven core principles. Landsc Ecol 30:1805–1835
Hicke J, Johnson MC, Hayes JL, Preisler HK (2012) Effects of bark beetle-caused tree mortality on wildfire. For Ecol Manag 271:81–90
Hicke JA, Meddens AJH, Kolden CA (2015) Recent tree mortality in the Western United States from bark beetles and forest fires. For Sci 62:141–153
Hindmarch TD, Reid ML (2001) Thinning of mature lodgepole pine stands increases scolytid bark beetle abundance and diversity. Can J For Res 31:1502–1512
Hoffman CM, Morgan P, Mell W, Parsons R, Strand E, Cook S (2012) Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. For Sci 59:390–399
Hoffman C, Parsons R, Morgan P, Mell R (2012b) Numerical simulation of crown fire hazard following bark beetle-caused mortality in lodgepole pine forests. For Sci 58(2):178–188
Hogg EH, Brandt JP, Kochtubajda B (2002) Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. Can J For Res 32:823–832
Hollaus M, Vreugdenhil M (2019) Radar satellite imagery for detecting bark beetle outbreaks in forests. Curr For Rep 5:240–250

Holopainen JK, Mustaniemi A, Kainulainen P, Satka H, Oksanen J (1993) Conifer aphids in an air-polluted environment. I. Aphid density, growth and accumulation of sulphur and nitrogen by scots pine and Norway spruce seedlings. Environ Pollut 80:185–191

Holton MK, Lindroth RL, Nordheim EV (2003) Foliar quality influences tree–herbivore–parasitoid interactions: effects of elevated CO_2, O_3, and plant genotype. Oecologia 137:233–244

Howe E, Baker WL (2003) Landscape heterogeneity and disturbance interactions in a subalpine watershed in Northern Colorado, USA. Ann Assoc Am Geogr 93:797–813

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Hummel S, Agee JK (2003) Western spruce budworm defoliation effects on forest structure and potential fire behavior. Northwest Sci 77:159–170

Hunter MD, Forkner RE (1999) Hurricane damage influences foliar polyphenolics and subsequent herbivory on surviving trees. Ecology 80:2676–2682

Itter MS, D'Orangeville L, Dawson A, Kneeshaw D, Duchesne L, Finley AO (2019) Boreal tree growth exhibits decadal-scale ecological memory to drought and insect defoliation, but no negative response to their interaction. J Ecol 107:1288–1301

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. Ecol Lett 10:835–848

Jaime L, Batllori E, Margalef-Marrase J, Pérez Navarro MÁ, Lloret F (2019) Scots pine (*Pinus sylvestris* L.) mortality is explained by the climatic suitability of both host tree and bark beetle populations. For Ecol Manag 448:119–129

James PMA, Fortin MJ, Sturtevant BR, Fall A, Kneeshaw D (2011) Modelling spatial interactions among fire, spruce budworm, and logging in the boreal forest. Ecosystems 14(1):60–75

James PMA, Robert LE, Wotton BM, Martell DL, Fleming RA (2017) Lagged cumulative spruce budworm defoliation affects the risk of fire ignition in Ontario, Canada. Ecol Appl 27:532–544

Jenkins MJ (2011) Fuel and fire behavior in high-elevation five-needle pines affected by mountain pine beetle. In: Future of high-elevation, five-needle white pines in Western North America, pp 198–205

Jenkins MJ, Runyon JB, Fettig CJ, Page WG, Bentz BJ (2014) Interactions among the mountain pine beetle, fires, and fuels. For Sci 60:489–501

Johansson T, Hjältén J, Gibb H, Hilszczanski J, Stenlid J, Ball JP, Alinvi O, Danell K (2007) Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: implications for conservation strategies. For Ecol Manag 242:496–510

Jolly WM, Parsons RA, Hadlow AM, Cohn GM, McAllister SS, Popp JB, Hubbard RM, Negron JF (2012) Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. For Ecol Manag 269:52–59

Jones ME, Hanlon CC, Paine TD (2015) Potential for interspecific competition between congeneric longhorned beetle species (Coleoptera: Cerambycidae) in an adventive environment. Environ Entomol 44:960–965

Jorgensen CA, Jenkins MJ (2010) Fuel complex alterations associated with spruce beetle-induced tree mortality in intermountain spruce-fir forests, USA. For Sci. https://doi.org/10.1093/forestscience/57.3.232

Joseph G, Kelsey RG, Peck RW, Niwa CG (2001) Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. J Chem Ecol 27:697–715

Keane RE, McKenzie D, Falk DA, Smithwick EAH, Miller C, Kellogg LKB (2015) Representing climate, disturbance, and vegetation interactions in landscape models. Ecol Model 309–310:33–47

Kelsey RG, Gallego D, Sánchez-García FJ, Pajares J (2014) Ethanol accumulation during severe drought may signal tree vulnerability to detection and attack by bark beetles. Can J For Res 44:554–561

Kelsey RG, Joseph G (2001) Attraction of *Scolytus unispinosus* bark beetles to ethanol in water-stressed Douglas-fir branches. For Ecol Manag 144:229–238

Kelsey RG, Joseph G (2003) Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can J For Res 33:870–884

Kelsey RG, Joseph G, Westlind D, Thies WG (2016) Ethanol and acetone from Douglas-fir roots stressed by *Phellinus sulphurascens* infection: Implications for detecting diseased trees and for beetle host selection. For Ecol Manag 360:261–272

Kelsey RG, Manter DK (2004) Effect of Swiss needle cast on Douglas-fir stem ethanol and monoterpene concentrations, oleoresin flow, and host selection by the Douglas-fir beetle. For Ecol Manag 190:241–253

Kelsey RG, Westlind DJ (2017a) Ethanol and primary attraction of red turpentine beetle in fire stressed ponderosa pine. For Ecol Manag 396:44–54

Kelsey RG, Westlind DJ (2017b) Physiological stress and ethanol accumulation in tree stems and woody tissues at sublethal temperatures from fire. Bioscience 67:443–451

Kenaley S, Mathiasen R, Harner EJ (2008) Mortality associated with a bark beetle outbreak in dwarf mistletoe-infested ponderosa pine stands in Arizona. West J Appl For 23:113–120

Kennedy A, McCullough DG (2002) Phenology of the larger European pine shoot beetle *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) in relation to native bark beetles and natural enemies in pine stands. Environ Entomol 31:261–272

Kerns BK, Westlind DJ (2013) Effect of season and interval of prescribed burn on ponderosa pine butterfly defoliation patterns. Can J For Res 43:979–983

Kidd NAC (1990) The effects of simulated acid mist on the growth rates of conifer aphids and the implications for tree health. J Appl Entomol 110:524–529

Kingsolver JG, Arthur Woods H, Buckley LB, Potter KA, MacLean HJ, Higgins JK (2011) Complex life cycles and the responses of insects to climate change. Integr Comp Biol 51:719–732

Kinney KK, Lindroth RL, Jung SM, Nordheim EV (1997) Effects of CO_2 and NO_3-availability on deciduous trees: phytochemistry and insect performance. Ecology 78:215–230

Kiritani K (2007) The impact of global warming and land-use change on the pest status of rice and fruit bugs (Heteroptera) in Japan. Glob Change Biol 13:1586–1595

Klutsch JG, Battaglia MA, West DR, Costello SL, Negrón JF (2011) Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. West J Appl For 26:101–109.

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. https://doi.org/10.7939/DVN

Koh LP (2007) Impacts of land use change on South-east Asian forest butterflies: a review. J Appl Ecol 44:703–713

Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. For Ecol Manag 380:321–334

Kopper BJ, Klepzig KD, Raffa KF (2004) Components of antagonism and mutualism in *Ips pini*–fungal interactions: relationship to a life history of colonizing highly stressed and dead trees. Environ Entomol 33:28–34

Kopper BJ, Lindroth RL (2003) Responses of trembling aspen (*Populus tremuloides*) phytochemistry and Aspen blotch leafminer (*Phyllonorycter tremuloidiella*) performance to elevated levels of atmospheric CO_2 and O_3. Agric For Entomol 5:17–26

Korasaki V, Braga RF, Zanetti R, Moreira FMS, Vaz-de-Mello FZ, Louzada J (2013) Conservation value of alternative land-use systems for dung beetles in Amazon: valuing traditional farming practices. Biodivers Conserv 22:1485–1499

Kozlov MV, Zverev V, Zvereva EL (2017) Combined effects of environmental disturbance and climate warming on insect herbivory in mountain birch in subarctic forests: results of 26-year monitoring. Sci Total Environ 601–602:802–811

Kulakowski D, Jarvis D (2011) The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: a look at the past century. For Ecol Manag 262:1686–1696

Kulakowski D, Jarvis D (2013) Low-severity fires increase susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. For Ecol Manag 289:544–550

Kulakowski D, Jarvis D, Veblen TT, Smith J (2012) Stand-replacing fires reduce susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado. J Biogeogr 39:2052–2060

Kulakowski D, Matthews C, Jarvis D, Veblen TT (2013) Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). J Veg Sci 24:168–176

Kulakowski D, Veblen TT (2007) Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88:759–769

Kulakowski D, Veblen TT, Bebi P (2003) Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. J Biogeogr 30:1445–1456

Kulakowski D, Veblen TT, Beb P (2016) Fire severity controlled susceptibility to a 1940s spruce beetle outbreak in Colorado, USA. PLoS ONE 11:1–16

Labandeira CC (2013) Deep-time patterns of tissue consumption by terrestrial arthropod herbivores. Naturwissenschaften 100:355–364

Land AD, Rieske LK (2006) Interactions among prescribed fire, herbivore pressure and shortleaf pine (*Pinus echinata*) regeneration following southern pine beetle (*Dendroctonus frontalis*) mortality. For Ecol Manag 235:260–269

Larsson S, Björkman C (1993) Performance of chewing and phloem-feeding insects on stressed trees. Scand J For Res 8:550–559

Leite MCA, Chen-Charpentier B, Agusto FB (2018) Maximizing tree harvesting benefit from forests under insect infestation disturbances. PLoS ONE. https://doi.org/10.1371/journal.pone.0200575

Leverkus AB, Lindenmayer DB, Thorn S, Gustafsson L (2018) Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. Glob Ecol Biogeogr 27:1140–1154

Liang L, Hawbaker TJ, Zhu Z, Li X, Gong P (2016) Forest disturbance interactions and successional pathways in the Southern Rocky Mountains. For Ecol Manag 375:35–45

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

Linn RR, Sieg CH, Hoffman CM, Winterkamp JL, McMillin JD (2013) Modeling wind fields and fire propagation following bark beetle outbreaks in spatially-heterogeneous pinyon-juniper woodland fuel complexes. Agric For Meteorol 173:139–153

Lloret F, Kitzberger T (2018) Historical and event-based bioclimatic suitability predicts regional forest vulnerability to compound effects of severe drought and bark beetle infestation. Glob Change Biol 24:1952–1964

Loch AD, Matsuki M (2010) Effects of defoliation by *Eucalyptus weevil*, *Gonipterus scutellatus*, and chrysomelid beetles on growth of *Eucalyptus globulus* in southwestern Australia. For Ecol Manag 260:1324–1332

Loehman RA, Keane RE, Holsinger LM, Wu Z (2017) Interactions of landscape disturbances and climate change dictate ecological pattern and process: spatial modeling of wildfire, insect, and disease dynamics under future climates. Landsc Ecol 32:1447–1459

Lombardero MJ, Ayres MP (2011) Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. Environ Entomol 40:1007–1018

Lombardero MJ, Ayres MP, Ayres BD (2006) Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. For Ecol Manag 225:349–358

Louis M, Grégoire JC, Pélisson PF (2014) Exploiting fugitive resources: How long-lived is "fugitive"? Fallen trees are a long-lasting reward for *Ips typographus* (Coleoptera, Curculionidae, Scolytinae). For Ecol Manag 331:129–134

Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience 56:395

Lucash MS, Scheller RM, Sturtevant BR, Gustafson EJ, Kretchun AM, Foster JR (2018) More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. Ecosphere. https://doi.org/10.1002/ecs2.2293
Lusebrink I, Evenden ML, Blanchet FG, Cooke JEK, Erbilgin N (2011) Effect of water stress and fungal inoculation on monoterpene emission from an historical and a new pine host of the mountain pine beetle. J Chem Ecol 37:1013–1026
Lynch HJ, Moorcroft PR (2008) A spatiotemporal Ripley's *K*-function to analyze interactions between spruce budworm and fire in British Columbia, Canada. Can J For Res 38:3112–3119
Lynch HJ, Renkin RA, Crabtree RL, Moorcroft PR (2006) The influence of previous mountain pine beetle (*Dendroctonus ponderosae*) activity on the 1988 Yellowstone fires. Ecosystems 9:1318–1327
Macquarrie CJK, Cooke BJ (2011) Density-dependent population dynamics of mountain pine beetle in thinned and unthinned stands. Can J For Res. https://doi.org/10.1139/x11-007
Maino JL, Kong JD, Hoffmann AA, Barton MG, Kearney MR (2016) Mechanistic models for predicting insect responses to climate change. Curr Opin Insect Sci 17:81–86
Makoto K, Kamata N, Kamibayashi N, Koike T, Tani H (2012) Bark-beetle-attacked trees produced more charcoal than unattacked trees during a forest fire on the Kenai Peninsula, Southern Alaska. Scand J For Res 27:30–35
Malesky DM, Bentz BJ, Brown GR, Brunelle AR, Buffington JM, Chappell LM, Derose RJ, Guyon JC, Jorgensen CL, Loehman RA, Lowrey LL, Lynch AM, Matyjasik M, Mcmillin JD, Mercado JE, Morris JL, Jose F, Padgett WG, Progar RA, Randall CB (2018) Effects of climate change on ecological disturbances. In: Climate change vulnerability and adaptation in the intermountain region: Part II. Gen. Tech. Rep. RMRS-GTR-375. US Department of Agriculture, Forest Service, Fort Collins, pp 199–263
Maňák V, Björklund N, Lenoir L, Nordlander G (2015) The effect of red wood ant abundance on feeding damage by the pine weevil *Hylobius abietis*. Agric For Entomol 17:57–63
Maňák V, Nordenhem H, Björklund N, Lenoir L, Nordlander G (2013) Ants protect conifer seedlings from feeding damage by the pine weevil *Hylobius abietis*. Agric For Entomol 15:98–105
Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, Grégoire JC, 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 (Cph) 40:1426–1435
Maroschek M, Rammer W, Lexer MJ (2015) Using a novel assessment framework to evaluate protective functions and timber production in Austrian mountain forests under climate change. Reg Environ Change 15:1543–1555
Martini X, Hughes MA, Killiny N, George J, Lapointe SL, Smith JA, Stelinski LL (2017) The fungus *Raffaelea lauricola* modifies behavior of its symbiont and vector, the redbay ambrosia beetle (*Xyleborus glabratus*), by altering host plant volatile production. J Chem Ecol 43:519–531
McCarley TR, Kolden CA, Vaillant NM, Hudak AT, Smith AMS, Kreitler J (2017) Landscape-scale quantification of fire-induced change in canopy cover following mountain pine beetle outbreak and timber harvest. For Ecol Manag 391:164–175
McCullough DG, Werner RA, Neumann D (1998) Fire and insects in northern and boreal forest ecosystems of North America. Annu Rev Entomol 43:107–127
McDonald EP, Agrell J, Lindroth RL (1999) CO_2 and light effects on deciduous trees: growth, foliar chemistry, and insect performance. Oecologia 119:389–399
McDowell NG, Allen CD, Marshall L (2010) Growth, carbon-isotope discrimination, and drought-associated mortality across a *Pinus ponderosa* elevational transect. Glob Change Biol 16:399–415
McDowell MN, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? N Phytol. https://doi.org/10.1111/j.1469-8137.2008.02436.x
McNichol MBH, Montes CR, Barnes BF, Nowak JT, Villari C, Gandhi KJK (2019) Interactions between southern *Ips bark* beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality. For Ecol Manag 446:164–174
McNulty SG, Boggs JL (2010) A conceptual framework: redefining forest soil's critical acid loads under a changing climate. Environ Pollut 158:2053–2058
Meigs GW, Campbell JL, Zald HSJ, Bailey JD, Shaw DC, Kennedy RE (2015) Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6:art118
Meigs GW, Zald HSJ, Campbell JL, Keeton WS, Kennedy RE (2016) Do insect outbreaks reduce the severity of subsequent forest fires? Environ Res Lett. https://doi.org/10.1088/1748-9326/11/4/045008
Meijer SS, Whittaker RJ, Borges PAV (2011) The effects of land-use change on arthropod richness and abundance on Santa Maria Island (Azores): unmanaged plantations favour endemic beetles. J Insect Conserv 15:505–522
Menges ES, Deyrup MA (2001) Postfire survival in south Florida slash pine: interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. Int J Wildl Fire 10:53–63
Mietkiewicz N, Kulakowski D (2016) Relative importance of climate and mountain pine beetle outbreaks on the occurrence of large wildfires in the western USA. Ecol Appl 26:2523–2535
Mietkiewicz N, Kulakowski D, Veblen TT (2018) Pre-outbreak forest conditions mediate the effects of spruce beetle outbreaks on fuels in subalpine forests of Colorado. Ecol Appl 28:457–472
Millar CI, Stephenson NL (2015) Temperate forest health in an era of emerging megadisturbance. Science 80-:349
Miller A, Rusnock P (1993) The rise and fall of the silvicultural hypothesis in spruce budworm (*Choristoneura fumiferana*) management in eastern Canada. For Ecol Manag 61:171–189
Moise ERD, Lavigne MB, Johns RC (2019) Density has more influence than drought on spruce budworm (*Choristoneura fumiferana*) performance under outbreak conditions. For Ecol Manag 433:170–175

Morán-Ordóñez A, Roces-Díaz JV, Otsu K, Ameztegui A, Coll L, Lefevre F, Retana J, Brotons L (2018) The use of scenarios and models to evaluate the future of nature values and ecosystem services in Mediterranean forests. Reg Environ Change. https://doi.org/10.1007/s10113-018-1408-5

Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, Van Vuuren DP, Carter TR, Emori S, Kainuma M, Kram T, Meehl GA, Mitchell JFB, Nakicenovic N, Riahi K, Smith SJ, Stouffer RJ, Thomson AM, Weyant JP, Wilbanks TJ (2010) The next generation of scenarios for climate change research and assessment. Nature 463:747–756

Navarro L, Harvey AE, Ali A, Bergeron Y, Morin H (2018) A Holocene landscape dynamic multiproxy reconstruction: how do interactions between fire and insect outbreaks shape an ecosystem over long time scales? PLoS ONE 13:1–16

Negron F, Mcmillin JD, Anhold JA, Coulson D (2009) Bark beetle-caused mortality in a drought-affected ponderosa pine landscape. For Ecol Manag 257:1353–1362

Nitschke CR, Amoroso M, Coates KD, Astrup R (2012) The influence of climate change, site type, and disturbance on stand dynamics in northwest British Columbia, Canada. Ecosphere 3:art11

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 For 113:454–462

O'Connor CD, Lynch AM, Falk DA, Swetnam TW (2015) Post-fire forest dynamics and climate variability affect spatial and temporal properties of spruce beetle outbreaks on a Sky Island mountain range. For Ecol Manag 336:148–162

Økland B, Nikolov C, Krokene P, Vakula J (2016) Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. For Ecol Manag 363:63–73

Page W, Jenkins MJ (2007a) Predicted fire behavior in selected mountain pine beetle-infested lodgepole pine. For Sci 53:662–674

Page WG, Jenkins MJ (2007b) Mountain pine beetle-induced changes to selected lodgepole pine fuel complexes within the intermountain region. For Sci 53:507–518

Palokangas P, Neuvonen S (1995) The effects of simulated acid rain on growth and susceptibility to predation *Phratora polaris* (Col., Chrysomelidae). Environ Pollut 89:67–71

Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric For Entomol 8:167–189

Pausas JG, Llovet J, Anselm R, Vallejo R (2008) Are wildfires a disaster in the Mediterranean basin? A review Vegetation changes Shrublands dominated by resprouting species. Int J Wildl Fire 17:713–723

Pawson SM, Marcot BG, Woodberry OG (2017) Predicting forest insect flight activity: a Bayesian network approach. PLoS ONE 12:1–23

Pechony O, Shindell DT (2010) Driving forces of global wildfires over the past millennium and the forthcoming century. Proc Natl Acad Sci USA 107:19167–19170

Percy K, Awmack C, Lindroth R, Kubiske M, Kopper B, Isebrands J, Pregitzer K, Hendrey G, Dickson R, Zak D, Oksanen E, Sober J, Harrington R, Karnosky D (2002) Altered performance of forest pests under atmospheres enriched by CO_2 and O_3. Nature 420:403–408

Perera AH, Sturtevant BR, Buse LJ (2015) Simulation modeling of forest landscape disturbances: an overview. In: Simulation modeling of forest landscape disturbances. Springer, Cham, pp 1–15

Perovich C, Sibold JS (2016) Forest composition change after a mountain pine beetle outbreak, Rocky Mountain National Park, CO, USA. For Ecol Manag 366:184–192

Perrakis DDB, Lanoville R, Taylor SW, Hicks D (2014) Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia, Canada. Fire Ecol 10:10–35

Peters DPC, Bestelmeyer BT, Turner MG (2007) Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Ecosystems 10:790–796

Pinna C, Linaldeddu BT, Deiana V, Maddau L, Montecchio L, Lentini A (2019) Plant pathogenic fungi associated with *Coraebus florentinus* (Coleoptera: Buprestidae) attacks in declining oak forests. Forests. https://doi.org/10.3390/f10060488

Pohl K, Hadley KS, Arabas KB (2006) Decoupling tree-ring signatures of climate variation, fire, and insect outbreaks in Central Oregon. Tree-Ring Res 62:37–50

Potterf M, Bone C (2017) Simulating bark beetle population dynamics in response to windthrow events. Ecol Complex 32:21–30

Powell EN, Townsend PA, Raffa KF (2012) Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle. Ecol Monogr 82:69–84

Prichard SJ, Kennedy MC (2014) Fuel treatments and landform modify landscape patterns of burn severity in an extreme fire event. Ecol Appl 24:571–590

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon PW, Desprez-Loustau ML, Nentwig W, Pergl J, Poboljšaj K, Rabitschi W, Roques A, Royr DB, Shirleys S, Solarzt W, Vilàu M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proc Natl Acad Sci USA 107:12157–12162

Radeloff VC, Mladenoff DJ, Boyce MS (2000) Effects of interacting disturbances on landscape patterns: budworm defoliation and salvage logging. Ecol Appl 10:233–247)

Radl A, Lexer MJ, Vacik H (2017) A Bayesian belief network approach to predict damages caused by disturbance agents. Forests. https://doi.org/10.3390/f9010015

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

Rankin LJ, Borden JH (1991) Competitive interaction between the mountain pine beetle and the pine engraver in lodgepole. Can J For Res 21:1029–1036

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reed SE, Juzwik J, English JT, Ginzel MD (2015) Colonization of artificially stressed black walnut trees by ambrosia beetle, bark beetle, and other weevil species (Coleoptera: Curculionidae) in Indiana and Missouri. Environ Entomol 44:1455–1464

Renwick KM, Rocca ME, Stohlgren TJ (2016) Biotic disturbance facilitates range shift at the trailing but not the leading edge of lodgepole pine's altitudinal distribution. J Veg Sci 27:780–788

Restaino C, Young DJN, Estes B, Gross S, Wuenschel A, Meyer M, Safford H (2019) Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. Ecol Appl 29:1–14

Reyes GP, Kneeshaw D (2008) Moderate-severity disturbance dynamics in *Abies balsamea–Betula* spp. forests: the relative importance of disturbance type and local stand and site characteristics on woody vegetation response. Écoscience 15:241–249

Robert LE, Sturtevant BR, Cooke BJ, James PMA, Fortin MJ, Townsend PA, Wolter PT, Kneeshaw D (2018) Landscape host abundance and configuration regulate periodic outbreak behavior in spruce budworm *Choristoneura fumiferana*. Ecography (Cph) 41:1556–1571

Robert LE, Sturtevant BR, Kneeshaw D, James PMA, Fortin MJ, Wolter PT, Townsend PA, Cooke BJ (2020) Forest landscape structure influences the cyclic-eruptive spatial dynamics of forest tent caterpillar outbreaks. Ecosphere. https://doi.org/10.1002/ecs2.3096

Rogers BM, Jantz P, Goetz SJ (2017) Vulnerability of eastern US tree species to climate change. Glob Change Biol 23:3302–3320

Rosenberger DW, Venette RC, Aukema BH (2017) Development of an aggressive bark beetle on novel hosts: implications for outbreaks in an invaded range. J Appl Ecol 55:1526–1537

Rossi FJ, Carter DR, Alavalapati JRR, Nowak JT (2011) Assessing landowner preferences for forest management practices to prevent the southern pine beetle: an attribute-based choice experiment approach. For Policy Econ 13:234–241

Rossi S, Plourde P-Y, Krause C (2018) Does a spruce budworm outbreak affect the growth response of black spruce to a subsequent thinning? Front Plant Sci 9:1–8

Roth SK, Lindroth RL (1994) Effects of CO_2-mediated changes in paper birch and white pine chemistry on gypsy moth performance. Oecologia 98:133–138

Roth S, Lindroth RL, Volin JC, Kruger EL (1998) Enriched atmospheric CO_2 and defoliation: effects on. Glob Change Biol. https://doi.org/10.1046/j.1365-2486.1998.00164.x

Rouault G, Candau J-N, Lieutier F, Nageleisen L-M, Martin J-C, Warzée N (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Ann For Sci 63:613–624

Ryan KC, Amman GD (1996) Bark beetle activity and delayed tree mortality in the greater Yellowstone area following the 1988 Fires. In: Ecological implications of fire in Greater Yellowstone proceedings. International Association of Wildland Fire, Fairland, pp 151–158

Saikkonen KT, Neuvonen S (1993) Effects of larval age and prolonged simulated acid rain on the susceptibility of European pine sawfly to virus infection. Oecologia 95:134–139

Saikkonen K, Neuvonen S, Kainulainen P (1995) Oviposition and larval performance of European pine sawfly in relation to irrigation, simulated acid rain and resin acid concentration in Scots pine. Oikos 74:273–282

Sangüesa-Barreda G, Linares JC, Camarero JJ (2015) Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: connecting climatic and biotic drivers of forest dieback. For Ecol Manag 357:126–137

Santoro AE, Lombardero MJ, Ayres MP, Ruel JJ (2001) Interactions between fire and bark beetles in an old growth pine forest. For Ecol Manag 144:245–254

Scheller RM, Kretchun AM, Loudermilk EL, Hurteau MD, Weisberg PJ, Skinner C (2018) Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the Lake Tahoe basin. Ecosystems 21:643–656

Schoennagel T, Veblen TT, Negron JF, Smith JM (2012) Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE. https://doi.org/10.1371/journal.pone.0030002

Schwab O, Maness T, Bull G, Welham C, Seely B, Blanco J (2011) Modeling the timber supply impact of introducing weevil-resistant spruce in British Columbia with cellular automata. For Policy Econ 13:61–68

Schwartzberg EG, Jamieson MA, Raffa KF, Reich PB, Montgomery RA, Lindroth RL (2014) Simulated climate warming alters phenological synchrony between an outbreak insect herbivore and host trees. Oecologia 175:1041–1049

Schwilk DW, Knapp EE, Ferrenberg SM, Keeley JE, Caprio AC (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For Ecol Manag 232:36–45

Seidl R, Donato DC, Raffa KF, Turner MG (2016) Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proc Natl Acad Sci USA 113:13075–13080

Seidl R, Rammer W (2017) Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. Landsc Ecol 32:1485–1498

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

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyer CPO (2017) Forest disturbances under climate change. Nat Clim Change 7:395–402

Shanahan E, Irvine KM, Thoma D, Wilmoth S, Ray A, Legg K, Shovic H (2016) Whitebark pine mortality related to white pine blister rust, mountain pine beetle outbreak, and water availability. Ecosphere. https://doi.org/10.1002/ecs2.1610

Sieg CH, Linn RR, Pimont F, Hoffman CM, McMillin JD, Winterkamp J, Baggett LS (2017) Fires following bark beetles: factors controlling severity and disturbance interactions in ponderosa pine. Fire Ecol 13:1–23

Simard M, Lajeunesse P (2015) The interaction between insect outbreaks and debris slides in a glacial valley of the Eastern Canadian Shield. Ecosystems 18:1281–1289

Simard M, Romme WH, Griffin JM, Turner MG (2011) Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol Monogr 81:3–24

Smith AL, Hewitt N, Klenk N, Bazely DR, Yan N, Wood S, Henriques I, MacLellan JI, Lipsig-Mummé C (2012) Effects of climate change on the distribution of invasive alien species in Canada: a knowledge synthesis of range change projections in a warming world. Environ Rev 20:1–16

Smith MJ, Weinberger C, Bruna EM, Allesina S (2014) The scientific impact of nations: journal placement and citation performance. PLoS ONE 9:1–6

Speer JH, Kulakowski D (2017) Creating a buzz: insect outbreaks and disturbance interactions. Dendroecology: https://doi.org/10.4135/9781446247501.n1010

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 Manag 318:167–174

Stevens-Rumann C, Morgan P, Chad H (2015) Bark beetles and wildfires: how does forest recovery change with repeated disturbances in mixed conifer forests? Ecosphere 6:art100

Stiling P, Rossy AM, Hungate B, Dukstra P, Hinkle CR, Knott WM, Drake B (1999) Decreased leaf-miner abundance in elevated CO_2: reduced leaf quality and increased parasitoid attack. Ecol Appl 9:240–244

Sturtevant BR, Miranda BR, Shinneman DJ, Gustafson EJ, Wolter PT, Sturtevant B, Miranda BR, Shinneman DJ, Gustafson EJ, Wolter PT (2012) Comparing modern and presettlement forest dynamics of a subboreal wilderness: does spruce budworm enhance fire risk? Ecol Appl 22:1278–1296

Su Q, NacLean DA, Needham TD (1996) The influence of hardwood content on balsam fir defoliation by spruce budworm. Can J For Res 26:1620–1628

Suárez-Vidal E, Sampedro L, Voltas J, Serrano L, Notivol E, Zas R (2019) Drought stress modifies early effective resistance and induced chemical defences of Aleppo pine against a chewing insect herbivore. Environ Exp Bot 162:550–559

Tabacaru CA, Erbilgin N (2015) Competitors and natural enemies may cumulatively mediate *Dendroctonus ponderosae* colonization of burned Pinus forests. For Ecol Manag 337:98–109

Tabacaru CA, McPike SM, Erbilgin N (2015) Fire-mediated interactions between a tree-killing bark beetle and its competitors. For Ecol Manag 356:262–272

Tabacaru CA, Park J, Erbilgin N (2016) Prescribed fire does not promote outbreaks of a primary bark beetle at low-density populations. J Appl Ecol 53:222–232

Talucci AC, Krawchuk M (2019) Dead forests burning: the influence of beetle outbreaks on fire severity and legacy structure in sub-boreal forests. Ecosphere 10:e02744

Taylor AR, Chen HYH, VanDamme L (2009) A review of forest succession models and their suitability for forest management planning. For Sci 55:23–36

Temperli C, Bugmann H, Elkin C (2013) Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. Ecol Monogr 83:383–402

Temperli C, Hart SJ, Veblen TT, Kulakowski D, Hicks JJ, Andrus R (2014) Are density reduction treatments effective at managing for resistance or resilience to spruce beetle disturbance in the southern Rocky Mountains? For Ecol Manag 334:53–63

Temperli C, Veblen TT, Hart SJ, Kulakowski D, Tepley AJ (2015) Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model. Ecosphere 6:1–20

Thistle HW, Peterson HG, Allwine G, Edburg SL, Lamb BK, Strom BL (2005) Pheromone movement in four stand thinning scenarios: high frequency plume observations. Pap. 051002. American Society of Agricultural Engineers, St. Joseph, Mich

Thom D, Rammer W, Seidl R (2017) Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. Glob Change Biol 23:269–282

Thom D, Seidl R, Steyrer G, Krehan H, Formayer H (2013) Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. For Ecol Manag 307:293–302

Torres-Muros L, Hódar JA, Zamora R (2017) Effect of habitat type and soil moisture on pupal stage of a Mediterranean forest pest (*Thaumetopoea pityocampa*). Agric For Entomol 19:130–138

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

van Lierop P, Lindquist E, Sathyapala S, Franceschini G (2015) Global forest area disturbance from fire, insect pests, diseases and severe weather events. For Ecol Manag 352:78–88

Veblen TT, Hadley KS, Nel EM, Kitzberger T, Reid M, Villalba R (2006) Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. J Ecol 82:125

Vepakomma U, Kneeshaw D, St-Onge B (2010) Interactions of multiple disturbances in shaping boreal forest dynamics: a spatially explicit analysis using multi-temporal LiDAR data and high-resolution imagery. J Ecol 98:526–539

Verble RM, Stephan FM (2009) Occurrence of carpenter ants in Ozark forests in relation to prescribed fire and stand variables. South J Appl For 33:42–45

Ward SF, Kees AM, Maddox MP, Montgomery RA, Aukema BH (2019) The role of simulated spring water stress in interactions between eastern larch and larch casebearer. Arthropod Plant Interact 13:621–633

Ward NL, Masters GJ (2007) Linking climate change and species invasion: an illustration using insect herbivores. Glob Change Biol 13:1605–1615

Watt GA, Fleming RA, Smith SM, Fortin MJ (2018) Spruce budworm (*Choristoneura fumiferana* Clem.) defoliation promotes vertical fuel continuity in Ontario's boreal mixedwood forest. Forests. https://doi.org/10.3390/f9050256

Watt GA, Stocks BJ, Fleming RA, Smith SM (2020) Stand breakdown and surface fuel accumulation due to spruce budworm (*Choristoneura fumiferana*) defoliation in the boreal mixedwood forest of central Canada. Can J For Res 9:1–9

Weed AS, Ayres MP, Hicke JA, Weed AS, Ayres MP, Hicke JA (2013) Consequences of climate change for biotic disturbances in North American forests. Ecol Monogr 83:441–470

Wermelinger B, Rigling A, Schneider Mathis D, Dobbertin M (2008) Assessing the role of bark- and wood-boring insects in the decline of Scots pine (*Pinus sylvestris*) in the Swiss Rhone valley. Ecol Entomol 33:239–249

Westlind DJ, Kelsey RG (2019) Predicting post-fire attack of red turpentine or western pine beetle on ponderosa pine and its impact on mortality probability in Pacific Northwest forests. For Ecol Manag 434:181–192

White PS, Pickett ST (1985) In: Pickett STA, White PSA (eds) The ecology of natural disturbance and patch dynamics. Academic Press, pp 3–13

Williams RS, Lincoln DE, Thomas RB (1994) Loblolly pine grown under elevated CO_2 affects early instar pine sawfly performance. Oecologia 98:64–71

Wong CM, Daniels LD (2017) Novel forest decline triggered by multiple interactions among climate, an introduced pathogen and bark beetles. Glob Change Biol 23:1926–1941

Woolley T, Shaw DC, Hollingsworth LT, Agne MC, Fitzgerald S, Eglitis A, Kurth L (2019) Beyond red crowns: complex changes in surface and crown fuels and their interactions 32 years following mountain pine beetle epidemics in south-central Oregon, USA. Fire Ecol. https://doi.org/10.1186/s42408-018-0010-z

Xu J, Budde KB, Hansen OK, Thomsen IM, Ravn HP, Nielsen UB (2018) Do silver fir woolly adelgids (*Dreyfusia nordmannianae*) facilitate pathogen infestation with *Neonectria neomacrospora* on Christmas trees (*Abies nordmanniana*)? For Ecol Manag 424:396–405

Yamazaki K (2011) Gone with the wind: trembling leaves may deter herbivory. Biol J Linn Soc 104:738–747

Yoneya K, Kugimiya S, Takabayashi J (2014) Leaf beetle larvae, *Plagiodera versicolora* (Coleoptera: Chrysomelidae), show decreased performance on uninfested host plants exposed to airborne factors from plants infested by conspecific larvae. Appl Entomol Zool 49:249–253

Zhang Q-H, Byers J, Zhang X-D (1993) Influence of bark thickness, trunk diameter and height on reproduction of the longhorned beetle, *Monochamus sutor* (Col., Cerambycidae) in burned larch and pine. J Appl Entomol 115:145–154