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Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling

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Summary

Drought has promoted large-scale, insect-induced tree mortality in recent years, with severe consequences for ecosystem function, atmospheric processes, sustainable resources and global biogeochemical cycles. However, the physiological linkages among drought, tree defences, and insect outbreaks are still uncertain, hindering our ability to accurately predict tree mortality under on-going climate change. Here we propose an interdisciplinary research agenda for addressing these crucial knowledge gaps. Our framework includes field manipulations, laboratory experiments, and modelling of insect and vegetation dynamics, and focuses on how drought affects interactions between conifer trees and bark beetles. We build upon existing theory and examine several key assumptions: 1) there is a trade-off in tree carbon investment between primary and secondary metabolites (e.g. growth vs. defence); 2) secondary metabolites are one of the main component of tree defence against bark beetles and associated microbes; and 3) implementing conifer-bark beetle interactions in current models improves predictions of forest disturbance in a changing climate. Our framework provides guidance for addressing a major shortcoming in current implementations of large-scale vegetation models, the under-representation of insect-induced tree mortality.

Key words: bark beetles; carbon allocation; climate changes; insects and pathogens; non-structural carbohydrate storage; secondary metabolites; tree mortality; vegetation models

Forests in a drying world

Forests provide vital ecosystem services ranging from commodities such as food and wood to ecological functions such as climate regulation and biodiversity conservation (Anderegg *et al.*, 2012). Yet, rapidly changing climate poses an increasing threat to global forest health (Trumbore *et al.*, 2015). For example, drought-related tree mortality events have been documented across all forested biomes (Allen *et al.*, 2015), and insect and pathogen outbreaks that often co-occur with drought have been reported as an important driver of forest decline (Kautz *et al.*, 2017).

As sessile organisms trees respond to drought and biotic attack by strategically allocating resources, e.g., carbon, nitrogen, and water, to the biosynthesis of a wide range of metabolic compounds. Compounds that are directly involved in growth, development, and reproduction are called primary metabolites, while secondary metabolites (SM) fulfil important functions such as herbivore deterrence (Mithöfer & Boland, 2012). Over the last decade the roles of primary carbon metabolism (e.g., assimilation, respiration, phloem transport) during tree mortality have received considerable attention (Adams *et al.*, 2017), while the mechanistic linkages between tree physiological processes and SM biosynthesis during drought remain only partially understood (McDowell *et al.*, 2013; Anderegg *et al.*, 2015).

Here we focus on drought impacts on physiological interactions of conifer species with bark beetles, the major mortality agents of conifer forests in China (Sun *et al.*, 2013), Europe (Seidl *et al.*, 2016), and North America (**Fig. 1**; Raffa *et al.*, 2008). We provide a brief overview of general aspects of carbon metabolism, including allocation of non-structural carbohydrates (NSC) to the biosynthesis of SM, and how this process may be influenced by drought. We then briefly review the current state of knowledge about conifer-bark beetle interactions, relate this to tree survival, and describe how tree defence and bark beetle infestations are currently simulated in models. Based on this synthesis, we develop a research agenda spanning field manipulations, laboratory experiments and vegetation modelling, which can bridge existing key knowledge gaps for improved predictions of tree mortality under climate change. This agenda focuses on 1) mechanistic linkages between drought, tree primary, and secondary metabolism; 2) the functional response of bark beetles to tree SM; and 3) integration of these relationships into nextgeneration vegetation models. Other aspects of climate change, such as elevated CO_2 (Robinson *et al.*, 2012) and temperature (Jamieson *et al.*, 2012), nutrient limitation (Björkman *et al.*, 1998) and flooding (Schroeder & Lindelöw, 2003), may dampen or amplify the complex interactions between trees and insects, but are beyond the scope of our assessment.

Carbon allocation to tree secondary metabolite biosynthesis

Carbon is assimilated by plant via photosynthetic uptake of atmospheric CO_2 (source activity) where solar energy is fixed in chemical bonds of carbon-rich compounds, particularly sugars and starch, referred to as NSC. These are then partitioned among several sinks within the plant, including respiration, structural growth, reproduction, storage and defence (**Fig. 2**). Carbon allocation is traditionally thought to be driven by the source-sink balance between carbon supply via photosynthesis and carbon demand for growth, a major sink that determines the availability of NSC for other demands (Le Roux *et al.*, 2001; Dietze *et al.*, 2014). For example, the "growth-differentiation balance hypothesis" (GDBH, Herms & Mattson, 1992) predicts that during environmental stress source activity initially outweighs sink activity and increases allocation to SM but, as stress persists or intensifies this balance shifts as more C is allocated to growth rather than to NSC and SM. While the GDBH has been validated for specific metabolic pathways, such as phenolics, and constitutive defence responses under some forms of stress, such as nutrient limitation (Koricheva *et al.*, 1998), we note that an increasing number of studies have found that allocation to terpenoids can increase concurrently with growth, contrary to the nonlinear relationships predicted by GDBH (Villari *et al.*, 2014; Klutsch & Erbilgin, 2018).

Functional trade-offs between primary and secondary metabolism in trees

We propose that the dynamics of SM are driven by a functional trade-off (*sensu* active storage; Dietze *et al.*, 2014) rather than solely by resource availability. Carbon investment is coordinated between primary (growth, respiration, and osmoregulation via NSC) and secondary metabolism (protection and defence via SM) in response to environmental and internal cues (**Fig. 2**). Trees may preferentially allocate carbon to SM rather than to growth because their long lifespan increases the risk of exposure to periods of both abiotic (e.g. drought) and biotic stress (i.e. insect attacks and pathogen infection). Greenhouse studies with tree seedlings have revealed such a conservative strategy, with allocation to storage (Weber *et al.*, 2019) and constitutive SM (Huang *et al.*, 2019) prioritized over growth under carbon limitation. However, it remains unknown to what extent the allocation schemes in tree seedlings can be extrapolated to mature trees, with which bark beetles are associated in nature.

Conifer species can optimize their defence capacity through both constitutive (always present) SM that reduce the probability of successful herbivore attack, and induced SM that are newly-produced upon attack or wounding and are usually more effective against a particular herbivore (**Fig. 2**; Franceschi *et al.*, 2005; Kessler, 2015). Investment into induced SM occurs only when needed and therefore plants can avoid unnecessary cost in the absence of herbivores. However, the activation, synthesis and accumulation of combined constitutive and induced SM may be too slow to reach effective levels against mass-attacking beetles and prevent lethal damage, when populations are high (Boone *et al.*, 2011). In addition, field studies have shown that local NSC storage was used for production of induced SM in response to simulated or actual bark beetle attack (Raffa *et al.*, 2017; Roth *et al.*, 2018) or fungal infection (Goodsman *et al.*, 2013; Arango-Velez *et al.*, 2018), while NSC stored in distant organs could not be mobilized to attacked stem sections (Wiley *et al.*, 2016). Such results indicate that mobilization and transport of NSC play an important role in allocation to induced defence in conifers. We conclude that trees need to balance the trade-offs between growth, storage and multipartite defences, especially when environmental stress causes source limitation.

Drought impacts on the functional trade-offs

Recent meta-analyses of drought manipulations have revealed that reduced NSC during drought is common, particularly in the roots of conifers where 33.5% reduction was observed (Adams *et al.*, 2017; Li *et al.*, 2018). This response is often due to reduced starch, which can occur despite increased sugar concentrations – a finding consistent with the role of soluble sugars as osmolytes (Dietze *et al.*, 2014). Similar to NSC dynamics, SM response to drought is not consistent, and can vary with the timing and severity of drought, the age and size of the tree, the type and ontogeny of the organ, and the class of SM (Jamieson *et al.*, 2017; Holopainen *et al.*, 2018). The lack of concurrent assessments of NSC and SM in most drought experiments makes it difficult to mechanistically link SM dynamics to the carbon balance and to derive allocation trade-offs (Ryan *et al.*, 2015).

The relationship between NSC and SM during drought can also be altered by the presence of insects. Drought-induced sink limitation may lead to an increase in NSC which are available for both constitutive and induced SM. However, when severe drought causes source limitation, NSC are required for life-maintaining functions like respiration and osmoregulation and thus are less available for constitutive SM, but may be preferentially used for biosynthesis of induced SM once attack occurs. Unfortunately, empirical evidence on how severe drought influences the inducibility of SM is still rare because manipulations of both drought and biotic stress are challenging in the field.

The role of secondary metabolites in tree defence against bark beetles

Co-evolutionary interactions between plants and insects have given rise to an enormous variety of SM with complex modes of action. While a subcortical habitat provides nutrition and shelter for bark beetles, they must also contend with substantial constitutive and induced tree defences (Franceschi *et al.*, 2005; Erbilgin, 2019), which can repel or kill attacking beetles at the time of colonization. During pheromone-mediated mass attacks, bark beetles may overwhelm these defences by exploiting plant-derived compounds, and by introducing various microorganisms that can detoxify tree SM (**Table 1**).

Conifer-bark beetle interactions

Conifers have elaborate networks of ducts and glands that store large amounts of oleoresin, a viscous mixture of terpenes that confer anatomical and chemical components of defence (**Table 2**). Resin exudation can physically entomb or delay attacking beetles while delivering SM that can adversely affect multiple life history aspects of bark beetles and their symbionts. For example, at high concentrations, phloem monoterpenes kill bark beetles and their fungal and bacterial symbionts (Raffa, 2014; Chiu *et al.*, 2017). Interactions can be complex, as bark beetles exploit lower concentrations of monoterpenes as cues that facilitate host location, recognition, and acceptance. Furthermore, bark beetles exploit monoterpenes as stimulators, precursors, and synergists of aggregation pheromones (Blomquist *et al.*, 2010; Chiu *et al.*, 2018), and some beetle-associated bacteria degrade monoterpenes (Boone *et al.*, 2013), both of which introduce feedbacks factoring the beetles. In addition to monoterpenes, diterpenes exert strong antifungal activity against a broad range of species (**Table 2**). To date no sesquiterpenes have been shown to affect bark beetles or their symbionts, but future work on this group of compounds is needed.

In addition to terpenes, conifer phloem also contains a highly diverse array of phenolic compounds, such as stilbenes, flavonoids, vanilloids, hydroxycinnamic acids, lignans, condensed tannins, and others. Some flavonoids have shown to directly affect beetles by acting as anti-feedants (Hammerbacher *et al.*, 2019), and phenylpropanoid 4-allylanisole can inhibit attraction of several bark beetle species to their aggregation pheromone (Joseph *et al.*, 2001). Several soluble phenolics, such as stilbenes and some flavonoids, are fungicidal at high concentrations (**Table 2**). However, these relationships involve complex feedbacks, as some bark beetle symbionts can circumvent this anti-fungal activity through the bioconversion of phenolics to carbon sources for larvae in the dying phloem (Zhao *et al.*, 2019). Likewise, as of yet there is no evidence of anti-beetle or anti-symbiont activity for many of the phenolics present in conifer tissue, so a defence function cannot currently be ascribed for these.

Linking SM dynamics to tree defence against bark beetle attack

Higher concentrations of monoterpenes, particularly induced concentrations in response to challenge inoculations with beetle-vectored fungi that simulate beetle attack, have been shown to predict tree survival from bark beetle attack in a number of genera, including *Pinus, Abies,* and *Picea* (Raffa *et al.*, 2005; Zhao *et al.*, 2011; Schiebe *et al.*, 2012). In Norway spruce (*Picea abies*), enhanced resin flow and accumulation of multiple toxic terpenes induced by treatment with methyl jasmonate reduced colonization by the European spruce bark beetle (*Ips typographus*, Erbilgin *et al.*, 2006) and infection by the blue-stain fungus *(Endoconidiophora polonica*, Zeneli *et al.*, 2006). Similarly, increased induced resin flow and higher densities of resin ducts have been associated with higher tree survival in lodgepole (*Pinus contorta*), limber (*P. flexilis*) and loblolly (*P. taeda*) pines (Ferrenberg *et al.*, 2014; Denham *et al.*, 2019). The relative proportions of monoterpene compounds have also been related to tree survival in some systems (Raffa *et al.*, 2005; Boone *et al.*, 2011; Erbilgin *et al.*, 2017). It should be noted that the key SM and their efficacies vary with systems (i.e. tree species, beetle species, fungal and bacterial species). Also, conifer-bark beetle dynamics are complicated by feedbacks arising from the cooperative behaviour of pheromone-mediated mass attacks, so the efficacy of both physical and chemical defences varies with beetle density (Boone *et al.*, 2011).

Drought has facilitated bark beetle outbreaks in central Europe and North America, resulting in regional scale mortality of spruce and pine forests (Meddens *et al.*, 2015; Seidl *et al.*, 2016). Experimental drought manipulations and field observations have related drought-related mortality to reduced resin flow (Netherer *et al.*, 2015) or reduced resin duct density and area (Gaylord *et al.*, 2013). Information on drought-induced changes in the composition of resins, volatile emissions and other defensive SM, is sparse (Ryan *et al.*, 2015). Even less is known about bark beetle-associated fungi, whose growth and germination rely on soluble sugars from living cells (Oliva *et al.*, 2014), but may also be inhibited by SM (**Table 2**). Therefore a depletion of NSC and SM during severe drought may result in contrasting effects on bark beetle-associated fungi.

Modelling tree defence and bark beetle infestations in dynamic vegetation models

Bark beetle infestations can be simulated across a wide range of spatial scales, from stand to continental. An increasing number of process-based infestation models have emerged over the last two decades (**Fig. 3**), addressing a variety of different bark beetle species, research questions, and management contexts (Seidl *et al.*, 2011). Historically, model development has progressed mainly in two directions. First, spatially-explicit agent-based models (ABMs) of bark beetles have been developed from principles established in earlier quantitative aggregation and attack models (Burnell, 1977; Berryman *et al.*, 1989). ABMs enable the detailed simulation of host-bark beetle interactions at the level of individual trees and beetles, and explicitly consider processes such as dispersal, tree defence, aggregation, and colonization explicitly (e.g., Kautz *et al.*, 2014; Honkaniemi *et al.*, 2018). However, ABMs are currently only applicable locally, and typically neglect vegetation dynamics and variation in climate. Second, model development has focused on integrating bark beetle dynamics into models of vegetation dynamics, specifically into forest landscape models (FLMs, Seidl & Rammer, 2017) and dynamic global vegetation models (DGVMs, Landry *et al.*, 2016). These developments are motivated by the growing awareness of the importance of bark beetles for vegetation dynamics (Running, 2008), and the high climate sensitivity of the host–bark beetle system (Raffa *et al.*, 2008). The level of process representation (e.g., insect development, dispersal and aggregation) in these integrated models, however, is usually lower than in the dedicated ABMs. In the following we will first show the effects of tree defence on simulated bark beetle dynamics, and subsequently review the current state-of-the-art in modelling tree defence to bark beetles.

Simulating the impact of tree defence on bark beetle infestations

An example for a DGVM simulating bark beetle infestation is the FATES-IMAP model (Functionally Assembled Terrestrial Ecosystem Simulator (Fisher *et al.*, 2015) coupled to an Insect Mortality and Phenology module (Goodsman *et al.*, 2018; **Method S1**). To gauge the effect that varying levels of tree vigour and defence have on vegetation-insect dynamics, we conducted simulation experiments in which we varied the incipient-epidemic threshold (i.e. the beetle population density that starts mass attacking healthy trees and is a proxy of tree defence) of the FATES-IMAP model in a stand undergoing a MPB outbreak (**Fig. 4**). When the incipient-epidemic threshold was decreased to the endemic MPB population level, all the appropriate host trees in the stand were quickly depleted in the simulation, whereas when the incipient epidemic threshold was increased, the outbreak duration increased while the outbreak severity decreased (**Fig. 4**). Low severity outbreaks could take a long time to deplete the hosts and thus increase the likelihood that the outbreak will be prematurely terminated by an extremely cold winter, as simulated bark beetle populations suffer high winter mortality that diminishes their populations to endemic levels. These simulation results imply that dynamically varying levels of tree defence (e.g., in response to changing drought regimes) could have profound impacts on outbreak trajectories, and consequently on projections of future vegetation dynamics.

Approaches to simulate tree defence against bark beetle infestation

In our comprehensive review of simulation models (**Method S2 and Table S3**), we found that how tree defence against bark beetles is considered in models varies widely, and ranges from detailed approaches linking a tree's physiological status to its defence capacity to not explicitly considering the process of tree defence in modelling (**Fig. 3**). In the majority of the models reviewed (74%), host susceptibility – i.e. the inverse of tree resistance and defence – is determined as a function of parameters related to vegetation structure, such as tree age, size, basal area, growth, and distance to previously infested trees (Seidl *et al.*, 2011). As tree susceptibility increases, the number of attacking beetles required for successful colonization is reduced (**Fig. 4**). A smaller subset of simulation approaches (21%), also explicitly considers climatic variables and their effect on tree defence and bark beetle susceptibility. Specifically, indicators of water usage and drought stress are employed, e.g., tree evapotranspiration relative to potential evapotranspiration (Temperli *et al.*, 2015). Other approaches to account for drought stress include a tree-specific threshold relating water demand to water supply (Jönsson *et al.*, 2012), or a climatic drought index (Scheller *et al.*, 2018). We found only one model (3%) relating defence capacity directly to a tree's physiological status, which simulated susceptibility as a function of the NSC reserves in individual host trees (Seidl & Rammer, 2017).

A research agenda for filling knowledge gaps toward more mechanistic predictions of bark beetle damage under drought

Lacking a detailed understanding of the physiological mechanisms by which tree defence and herbivores respond to drought, we have shown how modellers often rely on simplified metrics for simulations of tree-bark beetle interactions in vegetation models. Here, we identify three major knowledge gaps and propose research actions that can help inform future projections with more mechanistic insights. Although not exhaustive, the agenda outlined below would produce substantial progress toward understanding tree defence and bark beetle attack, and allow more accurate simulations of forest dynamics.

1. Determine mechanistic linkages between primary and secondary metabolism and their responses to drought (**Fig. 5 Partitioning**).

Action: Drought experiments and observational studies will be needed to achieve this objective. Hundreds of drought experiments have been conducted in recent years (Hoover *et al.*, 2018), but investigations have mostly focused on primary metabolisms. We propose to add new perspectives on defence metabolism into existing drought field experiments, specifically:

- Establish a standardized cross-calibrated protocol for sampling and analysing concentrations of NSC (e.g., soluble sugars and starch; Landhausser *et al.*, 2018) and SM (e.g., phenolics and terpenes) relevant for defence from a broad range of species and/or functional groups across a gradient of water availability. Archived sample material from previous drought studies can also be suitable for analysing concentrations of SM. Note that for volatile terpenoids samples should be stored under –80 °C.

- Normalize NSC and SM data within each species and field site before relating them, following the approach of Adams *et al.* (2017). Complementary data such as photosynthesis and growth are also needed to better understand the role of source vs. sink limitation on SM dynamics (Ryan *et al.*, 2015).

- Future in-situ drought studies should – where possible – apply isotope labelling (e.g., $^{13}CO_2$) to trace the flow of metabolites within the trees and from trees to insects, which can help identify the key physiological processes. This includes assessing the potential of phloem failure during drought to inhibit carbon transport to tissues attacked by bark beetles and pathogens (Sevanto, 2018); partitioning the relative contribution of newly-assimilated vs. old stored carbon to the production of SM (Huang *et al.*, 2018), and unravelling the role of terpenoids in anatomical and chemical components of tree defence.

2. Assess the role of secondary metabolites on the attack behaviour, development, and survival of bark beetles and their microbial associates as well as tree survival (**Fig. 5: Functioning**).

<u>Action</u>: Conduct laboratory assays and field surveys to identify the key defence compounds and how they influence bark beetle dynamics and tree survival.

- Bioassays with bark beetles at concentrations present in constitutive and induced phloem tissues will help determine which secondary compounds are bioactive among the vast array of compounds present. Behavioural assays should assess effects of both non-volatile compounds in bark and volatile compounds emitted by trees and fungi on beetle host selection and pheromone communication (Chiu *et al.*, 2018; Kandasamy *et al.*, 2019). Fitness assays can benefit from metrics of beetle life cycle (e.g. fecundity, growth rate, size, and survival) in combination with various levels of phloem nutritional quality and bioactive defence components.

- Field surveys are needed to establish the relationships of SM-based anatomical and chemical defence to bark beetle dynamics in different tree species that are attacked by different species of bark beetles and their associated microbiota. Within each species, resin flow, terpene chemistry and phenolic chemistry, should be analysed in mature trees that are subsequently not attacked or attacked, during endemic, transitory, and epidemic phases of bark beetles (Boone *et al.*, 2011; Amin *et al.*, 2013; Ghimire *et al.*, 2016). Note that analyses of total concentrations are more effective when focused on groups that have documented bioactivity, such as total monoterpenes or diterpenes rather than total terpenoids, and likewise to total stilbenes or phenylpropanoids rather than total phenolics.

3. Simulate drought-mediated tree defence against bark beetles by incorporating the functional mechanism derived from suggestions 1 and 2 (**Fig. 5: Modelling**).

Action: Implement the linkages between primary and secondary metabolism (and their responses to drought) as proxy mechanisms, where validated, for tree defence into vegetation models. This requires an improved physiological foundation in modelling vegetation dynamics, as many vegetation models still employ phenomenological or statistical approaches rather than first principles of ecophysiology for simulating vegetation growth and survival (Bugmann *et al.*, 2019).

- An explicit representation of physiology-based tree defence in large-scale models requires the consideration of species-specific differences in tree traits and physiology (rather than the use of plant functional types).

- Important thresholds of various tree-bark beetle systems, such as the number of beetles required to overcome trees defences, need to be made context-specific in models, accounting for the interactive effects of environmental drivers (e.g., drought) and beetle population dynamics (endemic vs. epidemic conditions).

- The multi-scaled nature of bark beetle outbreaks should be considered more explicitly in models, by simulating the cross-scale amplification that allows some beetle species to intermittently transition from killing individual or small patches of trees to killing trees across the spatial extent of subcontinents (Raffa *et al.*, 2008). A promising avenue of model development in this regard is the integration of ABM approaches (individual tree-beetle interactions) via carbon relations and defence metabolism into FLMs and DGVMs that are able to track ecosystem dynamics at the landscape to global scale.

- Better reference data for model calibration and evaluation are needed. Remote sensing data hold high potential in this regard, as they are becoming increasingly available and can provide long-term and consistent estimates of forest canopy mortality across large spatial extents (Senf *et al.*, 2018). However, improved attribution of mortality agents is needed for a consistent benchmarking of models against remotely sensed disturbance data (Kautz *et al.*, 2017). Additional data on insect populations are also needed for calibration of insect component for host-bark beetle interactions.

Conclusions and outlook

In this *Viewpoint* we propose an ambitious research agenda bridging carbon partitioning, defence functioning and vegetation modelling, which will provide substantial progress toward projecting future tree mortality from bark beetle outbreaks. Our synthesis strongly suggests that much knowledge necessary to improve vegetation models can be achieved through modification of existing research protocols and by capitalizing on the wealth of data and samples already collected from field manipulations. There are many aspects of climate-plant-insect interactions that have not been addressed here, in particular the interactive effects of drought, nutrient limitation, elevated CO_2 and temperature on carbon balance and allocation of NSC to SM; the role of volatile emissions for selection and aggregation of insects; and the interactions of insects and their associated microbiota. Many of these interactions are currently not well understood and should be addressed in future work to fully understand ecological impacts.

Our framework provides a mechanistic linkage between carbon allocation, which plays a key role in general plant responses to environmental changes (Mooney, 1972), and secondary metabolites, a critical and fundamental component of plant defence against insects and pathogens (Kessler, 2015). Thus, despite its focus on interactions between conifer species and bark beetles our research agenda also serves as a framework for improving the general understanding of plant-herbivore interactions and can be used as a blueprint for predicting other types of plant-insect system in a changing climate. Implementing our framework in other plant biological systems must take into account that impacts of climate change on carbon allocation to defence may vary among plant functional groups (e.g., evergreen vs deciduous, woody vs herbaceous plants) and with the mode of action of SM against different types of herbivores (e.g., defoliator vs stem borer). Also, the spatial and temporal scales at which a biological system operates will determine the type and structure of the most adequate vegetation model (e.g., ABM vs. FLM) for simulation and prediction. Implementing our research agenda in any plant-herbivore system will thus require interdisciplinary collaborations among ecologists, entomologists and vegetation modellers.

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Tables

Table 1 Major bark beetle species known to promote or cause significant mortality on conifers. Categorization of life history strategy is based on physiological condition of trees beetles commonly colonize, although this can vary with population phase (Raffa *et al.*, 1993). For an extensive list of species, please see Supporting Information Table S1.

Common name	**Scientific name**	**Common host**	**Known fungal symbionts**	**Life history strategy**
Southern Pine Beetle	*Dendroctonus frontalis*	*Pinus echinata,* *Pinus engelmanni,* *Pinus leiophylla,* *Pinus ponderosa,* *Pinus rigida,* *Pinus taeda,* *Pinus virginiana*	*Entomocorticium* sp. A, *Ceratocystiopsis ranaculosus*	Primary
Mountain Pine Beetle	*Dendroctonus ponderosae*	*Pinus contorta,* *Pinus ponderosa,* *Pinus albicaulis*	*Grosmannia clavigera,* *Ophiostoma montium,* *Leptographium longiclavatum,* *Entomocorticium dendroctoni*	Primary
North American Spruce beetle	*Dendroconus rufipennis*	*Picea engelmannii,* *Picea glauca,* *Picea sitchensis*	*Leptographium abietinum,* *Endoconidiophora rufipenni*	Primary
Piñon Ips	*Ips confusus*	*Pinus edulis,* *Pinus monophylla*		Secondary
European Spruce Bark Beetle	*Ips typographus*	*Picea abies*	*Endoconidiophora polonica ,* *Grosmannia penicillata,* *Grosmannia europhioides,* *Ophiostoma bicolor,* *Ophiostoma ainoae*	Primary

Table 2 Multiple chemical groups function in complementary fashion to inhibit bark beetle-fungal complexes. Modified from Raffa *et al.* (2005). For references, please see Supporting Information Table S2.

Biological effect	Monoterpenes	Diterpene acids	Phenolics
Adult repellency	++	?	+
Adult toxicity	++	?	+
Egg & larval toxicity	+	?	?
Pheromone inhibit	+	?	+
Microbial inhibition	+	+++	++

The biological effects of secondary metabolites are shown as inhibitory (+) or untested (?).

Figure captions

Figure 1 Cumulative tree mortality caused by mountain pine beetle (percent/1-km^2 grid cell) across the western United States (1997 – 2012) and British Columbia (2001 – 2010) from aerial survey data. The forest areas were adjusted according to Simard *et al.* (2011). The data presented here are the middle estimate (as detailed in Hicke *et al.* (2015) and Meddens *et al.* (2012)). In western US (1997-2012) and British Columbia (2001-2010), *c.* 3.04 and 5.10 millions of hectares of conifers has been killed by mountain pine beetles.

Figure 2 Schematic representation of how climate changes impact tree carbon allocation and its interactions with biotic agents such as bark beetles and pathogens. Under environmental stress like drought and heat, tree coordinate carbon supply via photosynthesis (1) and the demands for growth and reproduction (2), respiration (3), storage of non-structural carbohydrates (NSC) (4) and production of constitutive and induced secondary metabolites (CSM (5) and ISM (6), respectively). However, long-term severe stress can strongly limit photosynthesis and thus remobilization of storage compounds (7) may play an important role in allocation to tree defence. The production of CSM provides a first line of defence that allows repelling and/or poisoning insects and pathogens (8), while investment into ISM occurs after biotic attacks (9). Trees integrate constitutive and induced defence to enhance resistance to bark beetle-fungal complex (10), which in turn contend with tree defence by exploiting host monoterpenes (e.g., α-pinene) for production of aggregation pheromones and utilizing the host phenolic compounds (e.g., stilbenes and flavan-3-ols) as a carbon source (11). Figure adapted from Huang *et al.* (2019).

Figure 3 Distribution of bark beetle infestation models (n = 34) across three variables: bark beetle genus, implemented defence mechanism, and model type (DGVM = dynamic global vegetation model, FLM = forest landscape model, ABM = agent-based model). For the full list of models and methodological details see Table S3 and Methods S2 in the Supplementary Information. Flow width represents the number of models for each block of the three variables that are assigned to vertically-arranged axes. Both level of process detail in defence mechanism (centred axis) and spatial scope of the model type (right axis) typically increase from bottom to top. Structural parameters (e.g. tree age or size) play a major role in simulated tree defence yet, while climate-driven defence triggers (e.g. drought indices) are less frequent, and only one model explicitly accounts for tree physiology-based defence (NSC pool) against bark beetles.

Figure 4 Stand level trajectories for live trees larger than 20 cm diameter at breast height due to mountain pine beetle outbreaks simulated using the FATES-IMAP (Functionally Assembled Terrestrial Ecosystem Simulator – Insect Mortality and Phenology) model with different stand-level attack (incipient-epidemic) thresholds. This threshold is used as proxy for tree defence of all trees in a stand. The fitted estimate is approximately 343 beetles per ha, which corresponds to the trajectory with open circles. The endemic population level is 40 beetles per ha. When the incipient-epidemic threshold is decreased to the endemic population level, all suitable host trees in the stand are quickly depleted.

Figure 5 A simplified representation of framework showing the proposed three interdependent areas: (1) partitioning, that is, the trade-offs between primary and secondary metabolisms in a changing climate; 2) functioning, that is, the effectiveness of secondary metabolites, including constitutively expressed and also induced by biotic attacks (dashed line), on behaviour, development and survival of biotic agents (e.g. bark beetle and its associated fungi); (3) modelling, that is, the implementation of mechanistic relationships derived in 1) and 2) into current vegetation models.

Supporting Information

Table S1 A list of common beetle species known to promote or cause significant mortality on conifers

Table S2 Multiple chemical groups function in complementary fashion to inhibit bark beetle-fungal complexes.

Table S3 A list of the 34 bark beetle infestation models included in the review

Method S1 Description of the Insect Mortality and Phenology module incorporated into the FATES-IMAP

Method S2 Host tree defence implementation in process-based bark beetle models