

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

3 Authors:

4 Jianbei Huang<sup>1</sup>, Markus Kautz<sup>2</sup>, Amy M. Trowbridge<sup>3</sup>, Almuth Hammerbacher<sup>4,5</sup>, Kenneth F.  
5 Raffa<sup>6</sup>, Henry D. Adams<sup>7</sup>, Devin W. Goodsman<sup>8</sup>, Chonggang Xu<sup>9</sup>, Arjan J.H. Meddens<sup>10</sup>,  
6 Dineshkumar Kandasamy<sup>4</sup>, Jonathan Gershenson<sup>4</sup>, Rupert Seidl<sup>11</sup> and Henrik Hartmann<sup>1</sup>

7 Affiliations:

8 <sup>1</sup> Max Planck Institute for Biogeochemistry, Jena, Germany

9 <sup>2</sup> Department of Forest Health, Forest Research Institute Baden-Württemberg, Freiburg,  
10 Germany

11 <sup>3</sup> Department of Land Resources and Environmental Sciences, Montana State University,  
12 Bozeman, USA

13 <sup>4</sup> Max Planck Institute for Chemical Ecology, Jena, Germany

14 <sup>5</sup> Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute,  
15 University of Pretoria, Private Bag X20, 0028 Pretoria, South Africa

16 <sup>6</sup> Department of Entomology, University of Wisconsin, Madison, WI 53706, USA

17 <sup>7</sup> Department of Plant Biology, Ecology, and Evolution, Oklahoma State University, Stillwater, USA

18 <sup>8</sup> Natural Resources Canada, Canadian Forest Service, Victoria, BC, V8Z1M5, Canada

19 <sup>9</sup> Los Alamos National Laboratory, Los Alamos, NM 87545, USA

20 <sup>10</sup> Department of Natural Resources and Society, University of Idaho, Moscow, ID, USA

21 <sup>11</sup> Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural  
22 Resources and Life Sciences, Vienna, Austria

23 Author for correspondence: Jianbei Huang

24 Email: [hjianbei@bgc-jena.mpg.de](mailto:hjianbei@bgc-jena.mpg.de)

25 Total words: ~4200;

26 Tables and figures in main body: 2 tables and 5 figures.

27

## 28 **Summary**

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

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

## 46 **Forests in a drying world**

47 Forests provide vital ecosystem services ranging from commodities such as food and wood to  
48 ecological functions such as climate regulation and biodiversity conservation (Anderegg *et al.*,  
49 2012). Yet, rapidly changing climate poses an increasing threat to global forest health (Trumbore  
50 *et al.*, 2015). For example, drought-related tree mortality events have been documented across  
51 all forested biomes (Allen *et al.*, 2015), and insect and pathogen outbreaks that often co-occur  
52 with drought have been reported as an important driver of forest decline (Kautz *et al.*, 2017).

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

62 Here we focus on drought impacts on physiological interactions of conifer species with bark  
63 beetles, the major mortality agents of conifer forests in China (Sun *et al.*, 2013), Europe (Seidl *et al.*  
64 *et al.*, 2016), and North America (**Fig. 1**; Raffa *et al.*, 2008). We provide a brief overview of general  
65 aspects of carbon metabolism, including allocation of non-structural carbohydrates (NSC) to the  
66 biosynthesis of SM, and how this process may be influenced by drought. We then briefly review  
67 the current state of knowledge about conifer-bark beetle interactions, relate this to tree survival,  
68 and describe how tree defence and bark beetle infestations are currently simulated in models.  
69 Based on this synthesis, we develop a research agenda spanning field manipulations, laboratory  
70 experiments and vegetation modelling, which can bridge existing key knowledge gaps for  
71 improved predictions of tree mortality under climate change. This agenda focuses on 1)  
72 mechanistic linkages between drought, tree primary, and secondary metabolism; 2) the  
73 functional response of bark beetles to tree SM; and 3) integration of these relationships into next-

74 generation vegetation models. Other aspects of climate change, such as elevated CO<sub>2</sub> (Robinson  
75 *et al.*, 2012) and temperature (Jamieson *et al.*, 2012), nutrient limitation (Björkman *et al.*, 1998)  
76 and flooding (Schroeder & Lindelöw, 2003), may dampen or amplify the complex interactions  
77 between trees and insects, but are beyond the scope of our assessment.

## 78 **Carbon allocation to tree secondary metabolite biosynthesis**

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

## 94 *Functional trade-offs between primary and secondary metabolism in trees*

95 We propose that the dynamics of SM are driven by a functional trade-off (*sensu* active storage;  
96 Dietze *et al.*, 2014) rather than solely by resource availability. Carbon investment is coordinated  
97 between primary (growth, respiration, and osmoregulation via NSC) and secondary metabolism  
98 (protection and defence via SM) in response to environmental and internal cues (**Fig. 2**). Trees  
99 may preferentially allocate carbon to SM rather than to growth because their long lifespan  
100 increases the risk of exposure to periods of both abiotic (e.g. drought) and biotic stress (i.e. insect  
101 attacks and pathogen infection). Greenhouse studies with tree seedlings have revealed such a

102 conservative strategy, with allocation to storage (Weber *et al.*, 2019) and constitutive SM (Huang  
103 *et al.*, 2019) prioritized over growth under carbon limitation. However, it remains unknown to  
104 what extent the allocation schemes in tree seedlings can be extrapolated to mature trees, with  
105 which bark beetles are associated in nature.

106 Conifer species can optimize their defence capacity through both constitutive (always  
107 present) SM that reduce the probability of successful herbivore attack, and induced SM that are  
108 newly-produced upon attack or wounding and are usually more effective against a particular  
109 herbivore (**Fig. 2**; Franceschi *et al.*, 2005; Kessler, 2015). Investment into induced SM occurs only  
110 when needed and therefore plants can avoid unnecessary cost in the absence of herbivores.  
111 However, the activation, synthesis and accumulation of combined constitutive and induced SM  
112 may be too slow to reach effective levels against mass-attacking beetles and prevent lethal  
113 damage, when populations are high (Boone *et al.*, 2011). In addition, field studies have shown  
114 that local NSC storage was used for production of induced SM in response to simulated or actual  
115 bark beetle attack (Raffa *et al.*, 2017; Roth *et al.*, 2018) or fungal infection (Goodsman *et al.*,  
116 2013; Arango-Velez *et al.*, 2018), while NSC stored in distant organs could not be mobilized to  
117 attacked stem sections (Wiley *et al.*, 2016). Such results indicate that mobilization and transport  
118 of NSC play an important role in allocation to induced defence in conifers. We conclude that trees  
119 need to balance the trade-offs between growth, storage and multipartite defences, especially  
120 when environmental stress causes source limitation.

### 121 *Drought impacts on the functional trade-offs*

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

130 mechanistically link SM dynamics to the carbon balance and to derive allocation trade-offs (Ryan  
131 *et al.*, 2015).

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

#### 140 **The role of secondary metabolites in tree defence against bark beetles**

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

#### 148 *Conifer-bark beetle interactions*

149 Conifers have elaborate networks of ducts and glands that store large amounts of oleoresin, a  
150 viscous mixture of terpenes that confer anatomical and chemical components of defence (**Table**  
151 **2**). Resin exudation can physically entomb or delay attacking beetles while delivering SM that can  
152 adversely affect multiple life history aspects of bark beetles and their symbionts. For example, at  
153 high concentrations, phloem monoterpenes kill bark beetles and their fungal and bacterial  
154 symbionts (Raffa, 2014; Chiu *et al.*, 2017). Interactions can be complex, as bark beetles exploit  
155 lower concentrations of monoterpenes as cues that facilitate host location, recognition, and  
156 acceptance. Furthermore, bark beetles exploit monoterpenes as stimulators, precursors, and

157 synergists of aggregation pheromones (Blomquist *et al.*, 2010; Chiu *et al.*, 2018), and some  
158 beetle-associated bacteria degrade monoterpenes (Boone *et al.*, 2013), both of which introduce  
159 feedbacks factoring the beetles. In addition to monoterpenes, diterpenes exert strong antifungal  
160 activity against a broad range of species (**Table 2**). To date no sesquiterpenes have been shown  
161 to affect bark beetles or their symbionts, but future work on this group of compounds is needed.

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

### 173 *Linking SM dynamics to tree defence against bark beetle attack*

174 Higher concentrations of monoterpenes, particularly induced concentrations in response to  
175 challenge inoculations with beetle-vectored fungi that simulate beetle attack, have been shown  
176 to predict tree survival from bark beetle attack in a number of genera, including *Pinus*, *Abies*, and  
177 *Picea* (Raffa *et al.*, 2005; Zhao *et al.*, 2011; Schiebe *et al.*, 2012). In Norway spruce (*Picea abies*),  
178 enhanced resin flow and accumulation of multiple toxic terpenes induced by treatment with  
179 methyl jasmonate reduced colonization by the European spruce bark beetle (*Ips typographus*,  
180 Erbilgin *et al.*, 2006) and infection by the blue-stain fungus (*Endoconidiophora polonica*, Zeneli *et*  
181 *al.*, 2006). Similarly, increased induced resin flow and higher densities of resin ducts have been  
182 associated with higher tree survival in lodgepole (*Pinus contorta*), limber (*P. flexilis*) and loblolly  
183 (*P. taeda*) pines (Ferrenberg *et al.*, 2014; Denham *et al.*, 2019). The relative proportions of  
184 monoterpene compounds have also been related to tree survival in some systems (Raffa *et al.*,

185 2005; Boone *et al.*, 2011; Erbilgin *et al.*, 2017). It should be noted that the key SM and their  
186 efficacies vary with systems (i.e. tree species, beetle species, fungal and bacterial species). Also,  
187 conifer-bark beetle dynamics are complicated by feedbacks arising from the cooperative  
188 behaviour of pheromone-mediated mass attacks, so the efficacy of both physical and chemical  
189 defences varies with beetle density (Boone *et al.*, 2011).

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

### 199 **Modelling tree defence and bark beetle infestations in dynamic vegetation models**

200 Bark beetle infestations can be simulated across a wide range of spatial scales, from stand to  
201 continental. An increasing number of process-based infestation models have emerged over the  
202 last two decades (**Fig. 3**), addressing a variety of different bark beetle species, research questions,  
203 and management contexts (Seidl *et al.*, 2011). Historically, model development has progressed  
204 mainly in two directions. First, spatially-explicit agent-based models (ABMs) of bark beetles have  
205 been developed from principles established in earlier quantitative aggregation and attack models  
206 (Burnell, 1977; Berryman *et al.*, 1989). ABMs enable the detailed simulation of host-bark beetle  
207 interactions at the level of individual trees and beetles, and explicitly consider processes such as  
208 dispersal, tree defence, aggregation, and colonization explicitly (e.g., Kautz *et al.*, 2014;  
209 Honkaniemi *et al.*, 2018). However, ABMs are currently only applicable locally, and typically  
210 neglect vegetation dynamics and variation in climate. Second, model development has focused  
211 on integrating bark beetle dynamics into models of vegetation dynamics, specifically into forest  
212 landscape models (FLMs, Seidl & Rammer, 2017) and dynamic global vegetation models (DGVMs,



213 Landry *et al.*, 2016). These developments are motivated by the growing awareness of the  
214 importance of bark beetles for vegetation dynamics (Running, 2008), and the high climate  
215 sensitivity of the host–bark beetle system (Raffa *et al.*, 2008). The level of process representation  
216 (e.g., insect development, dispersal and aggregation) in these integrated models, however, is  
217 usually lower than in the dedicated ABMs. In the following we will first show the effects of tree  
218 defence on simulated bark beetle dynamics, and subsequently review the current state-of-the-  
219 art in modelling tree defence to bark beetles.

### 220 *Simulating the impact of tree defence on bark beetle infestations*

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

### 237 *Approaches to simulate tree defence against bark beetle infestation*

238 In our comprehensive review of simulation models (**Method S2 and Table S3**), we found that how  
239 tree defence against bark beetles is considered in models varies widely, and ranges from detailed  
240 approaches linking a tree's physiological status to its defence capacity to not explicitly

241 considering the process of tree defence in modelling (**Fig. 3**). In the majority of the models  
242 reviewed (74%), host susceptibility – i.e. the inverse of tree resistance and defence – is  
243 determined as a function of parameters related to vegetation structure, such as tree age, size,  
244 basal area, growth, and distance to previously infested trees (Seidl *et al.*, 2011). As tree  
245 susceptibility increases, the number of attacking beetles required for successful colonization is  
246 reduced (**Fig. 4**). A smaller subset of simulation approaches (21%), also explicitly considers  
247 climatic variables and their effect on tree defence and bark beetle susceptibility. Specifically,  
248 indicators of water usage and drought stress are employed, e.g., tree evapotranspiration relative  
249 to potential evapotranspiration (Temperli *et al.*, 2015). Other approaches to account for drought  
250 stress include a tree-specific threshold relating water demand to water supply (Jönsson *et al.*,  
251 2012), or a climatic drought index (Scheller *et al.*, 2018). We found only one model (3%) relating  
252 defence capacity directly to a tree’s physiological status, which simulated susceptibility as a  
253 function of the NSC reserves in individual host trees (Seidl & Rammer, 2017).

#### 254 **A research agenda for filling knowledge gaps toward more mechanistic predictions of bark** 255 **beetle damage under drought**

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

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

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

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

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

279 • Future in-situ drought studies should – where possible – apply isotope labelling (e.g.,  $^{13}\text{C}$ ) to  
280 trace the flow of metabolites within the trees and from trees to insects, which can help identify  
281 the key physiological processes. This includes assessing the potential of phloem failure during  
282 drought to inhibit carbon transport to tissues attacked by bark beetles and pathogens (Sevanto,  
283 2018); partitioning the relative contribution of newly-assimilated vs. old stored carbon to the  
284 production of SM (Huang *et al.*, 2018), and unravelling the role of terpenoids in anatomical and  
285 chemical components of tree defence.

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

288 Action: Conduct laboratory assays and field surveys to identify the key defence compounds and  
289 how they influence bark beetle dynamics and tree survival.

290 • Bioassays with bark beetles at concentrations present in constitutive and induced phloem  
291 tissues will help determine which secondary compounds are bioactive among the vast array of  
292 compounds present. Behavioural assays should assess effects of both non-volatile compounds in  
293 bark and volatile compounds emitted by trees and fungi on beetle host selection and pheromone  
294 communication (Chiu *et al.*, 2018; Kandasamy *et al.*, 2019). Fitness assays can benefit from

295 metrics of beetle life cycle (e.g. fecundity, growth rate, size, and survival) in combination with  
296 various levels of phloem nutritional quality and bioactive defence components.

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

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

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

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

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

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

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

### 334 **Conclusions and outlook**

335 In this *Viewpoint* we propose an ambitious research agenda bridging carbon partitioning, defence  
336 functioning and vegetation modelling, which will provide substantial progress toward projecting  
337 future tree mortality from bark beetle outbreaks. Our synthesis strongly suggests that much  
338 knowledge necessary to improve vegetation models can be achieved through modification of  
339 existing research protocols and by capitalizing on the wealth of data and samples already  
340 collected from field manipulations. There are many aspects of climate-plant-insect interactions  
341 that have not been addressed here, in particular the interactive effects of drought, nutrient  
342 limitation, elevated CO<sub>2</sub> and temperature on carbon balance and allocation of NSC to SM; the  
343 role of volatile emissions for selection and aggregation of insects; and the interactions of insects  
344 and their associated microbiota. Many of these interactions are currently not well understood  
345 and should be addressed in future work to fully understand ecological impacts.

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

361

## 362 **Acknowledgements**

363 JH, AH, DK, JG, and HH were funded by Max Planck Society. AMT and HDA were supported by the  
364 National Science Foundation, Division of Integrative Organismal Systems, Integrative Ecological  
365 Physiology Programme (no. 1755346). AMT recognizes contributions from the USDA National  
366 Institute of Food and Agriculture Hatch project (MONB00389). HDA recognizes support from the  
367 Office of the Vice President for Research at Oklahoma State University. RS acknowledges support  
368 from the Austrian Science Fund FWF through START grant Y895-B25. KFR acknowledges the  
369 University of Wisconsin-Madison Vilas-Sorenson Professorship from the College of Agricultural  
370 and Life Sciences the Graduate School. D.G was funded by the Los Alamos National Laboratory  
371 Centre for Space and Earth Science and Exploratory Research program. CX was funded by the UC-  
372 Lab Fees Research Program (grant nos. LFR18-542511).

## 373 **References**

- 374 **Adams HD, Zeppel MJB, Anderegg WRL, Hartmann H, Landhäuser SM, Tissue DT, Huxman TE, Hudson**  
 375 **PJ, Franz TE, Allen CD, et al. 2017.** A multi-species synthesis of physiological mechanisms in  
 376 drought-induced tree mortality. *Nature Ecology & Evolution* **1**: 1285-1291.
- 377 **Allen CD, Breshears DD, McDowell NG. 2015.** On underestimation of global vulnerability to tree  
 378 mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**: 129.
- 379 **Amin HS, Russo RS, Sive B, Richard Hoebeke E, Dodson C, McCubbin IB, Gannet Hallar A, Huff Hartz KE.**  
 380 **2013.** Monoterpene emissions from bark beetle infested Engelmann spruce trees. *Atmospheric*  
 381 *Environment* **72**: 130-133.
- 382 **Anderegg WRL, Kane JM, Anderegg LDL. 2012.** Consequences of widespread tree mortality triggered by  
 383 drought and temperature stress. *Nature Climate Change* **3**: 30-36.
- 384 **Anderegg WRL, Hicke JA, Fisher RA, Allen CD, Aukema J, Bentz B, Hood S, Lichstein JW, Macalady AK,**  
 385 **McDowell N, et al. 2015.** Tree mortality from drought, insects, and their interactions in a  
 386 changing climate. *New Phytologist* **208**: 674-683.
- 387 **Arango-Velez A, Chakraborty S, Blascyk K, Phan MT, Barsky J, El Kayal W. 2018.** Anatomical and  
 388 chemical responses of eastern white pine (*Pinus strobus* L.) to blue-stain (*Ophiostoma minus*)  
 389 inoculation. *Forests* **9**: 690.
- 390 **Berryman AA, Raffa KF, Millstein JA, Nils Chr S. 1989.** Interaction dynamics of bark beetle aggregation  
 391 and conifer defense rates. *Oikos* **56**: 256-263.
- 392 **Björkman C, Kytö M, Larsson S, Niemelä P. 1998.** Different responses of two carbon-based defences in  
 393 Scots pine needles to nitrogen fertilization. *Ecoscience* **5**: 502-507.
- 394 **Blomquist GJ, Figueroa-Teran R, Aw M, Song M, Gorzalski A, Abbott NL, Chang E, Tittiger C. 2010.**  
 395 Pheromone production in bark beetles. *Insect Biochemistry and Molecular Biology* **40**: 699-712.
- 396 **Boone CK, Aukema BH, Bohlmann J, Carroll AL, Raffa KF. 2011.** Efficacy of tree defense physiology  
 397 varies with bark beetle population density: a basis for positive feedback in eruptive species.  
 398 *Canadian Journal of Forest Research* **41**: 1174-1188.
- 399 **Boone CK, Keefover-Ring K, Mapes AC, Adams AS, Bohlmann J, Raffa KF. 2013.** Bacteria associated with  
 400 a tree-killing insect reduce concentrations of plant defense compounds. *Journal of Chemical*  
 401 *Ecology* **39**: 1003-1006.
- 402 **Bugmann H, Seidl R, Hartig F, Bohn F, Brūna J, Cailleret M, François L, Heinke J, Henrot A-J, Hickler T, et**  
 403 **al. 2019.** Tree mortality submodels drive simulated long-term forest dynamics: assessing 15  
 404 models from the stand to global scale. *Ecosphere*. doi: 10.1002/ecs2.2616
- 405 **Burnell DG. 1977.** A dispersal-aggregation model for mountain pine beetle in lodgepole pine stands.  
 406 *Researches on Population Ecology* **19**: 99-106.
- 407 **Chiu CC, Keeling CI, Bohlmann J. 2017.** Toxicity of pine monoterpenes to mountain pine beetle.  
 408 *Scientific Reports* **7**: 8858.
- 409 **Chiu CC, Keeling CI, Bohlmann J. 2018.** Monoterpenyl esters in juvenile mountain pine beetle and sex-  
 410 specific release of the aggregation pheromone *trans*-verbenol. *Proceedings of the National*  
 411 *Academy of Sciences* **115**: 3652-3657.
- 412 **Denham SO, Coyle DR, Oishi AC, Bullock BP, Heliövaara K, Novick KA. 2019.** Tree resin flow dynamics  
 413 during an experimentally induced attack by *Ips avulsus*, *I. calligraphus*, and *I. grandicollis*.  
 414 *Canadian Journal of Forest Research* **49**: 53-63.
- 415 **Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R. 2014.**  
 416 Nonstructural carbon in woody plants. *Annual Review of Plant Biology* **65**: 667-687.
- 417 **Erbilgin N, Krokene P, Christiansen E, Zeneli G, Gershenson J. 2006.** Exogenous application of methyl  
 418 jasmonate elicits defenses in Norway spruce (*Picea abies*) and reduces host colonization by the  
 419 bark beetle *Ips typographus*. *Oecologia* **148**: 426-436.

- 420 **Erbilgin N, Cale JA, Hussain A, Ishangulyyeva G, Klutsch JG, Najar A, Zhao S. 2017.** Weathering the  
 421 storm: how lodgepole pine trees survive mountain pine beetle outbreaks. *Oecologia* **184**: 469-  
 422 478.
- 423 **Erbilgin N. 2019.** Phytochemicals as mediators for host range expansion of a native invasive forest insect  
 424 herbivore. *New Phytologist* **221**: 1268-1278.
- 425 **Ferrenberg S, Kane JM, Mitton JB. 2014.** Resin duct characteristics associated with tree resistance to  
 426 bark beetles across lodgepole and limber pines. *Oecologia* **174**: 1283-1292.
- 427 **Fisher RA, Muszala S, Versteinstein M, Lawrence P, Xu C, McDowell NG, Knox RG, Koven C, Holm J,  
 428 Rogers BM, et al. 2015.** Taking off the training wheels: the properties of a dynamic vegetation  
 429 model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development* **8**: 3593-3619.
- 430 **Franceschi VR, Krokene P, Christiansen E, Krekling T. 2005.** Anatomical and chemical defenses of  
 431 conifer bark against bark beetles and other pests. *New Phytologist* **167**: 353-376.
- 432 **Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yopez EA, Macalady AK, Pangle RE, McDowell NG. 2013.**  
 433 Drought predisposes piñon–juniper woodlands to insect attacks and mortality. *New Phytologist*  
 434 **198**: 567-578.
- 435 **Ghimire RP, Kivimäenpää M, Blomqvist M, Holopainen T, Lyytikäinen-Saarenmaa P, Holopainen JK.  
 436 2016.** Effect of bark beetle (*Ips typographus* L.) attack on bark VOC emissions of Norway spruce  
 437 (*Picea abies* Karst.) trees. *Atmospheric Environment* **126**: 145-152.
- 438 **Goodsman DW, Lusebrink I, Landhäusser SM, Erbilgin N, Lieffers VJ. 2013.** Variation in carbon  
 439 availability, defense chemistry and susceptibility to fungal invasion along the stems of mature  
 440 trees. *New Phytologist* **197**: 586-594.
- 441 **Goodsman DW, Aukema BH, McDowell NG, Middleton RS, Xu C. 2018.** Incorporating variability in  
 442 simulations of seasonally forced phenology using integral projection models. *Ecology and  
 443 Evolution* **8**: 162-175.
- 444 **Hammerbacher A, Kandasamy D, Ullah C, Schmidt A, Wright LP, Gershenson J. 2019.** Flavanone-3-  
 445 Hydroxylase plays an important role in the biosynthesis of spruce phenolic defenses against bark  
 446 beetles and their fungal associates. *Frontiers in Plant Science* doi:10.3389/fpls.2019.00208
- 447 **Herms DA, Mattson WJ. 1992.** The dilemma of plants: to grow or defend. *The Quarterly Review of  
 448 Biology* **67**: 283-335.
- 449 **Hicke JA, Meddens AJH, Kolden CA. 2015.** Recent tree mortality in the Western United States from bark  
 450 beetles and forest fires. *Forest Science* **62**: 141-153.
- 451 **Holopainen JK, Virjamo V, Ghimire RP, Blande JD, Julkunen-Tiitto R, Kivimäenpää M. 2018.** Climate  
 452 change effects on secondary compounds of forest trees in the Northern Hemisphere. *Frontiers  
 453 in Plant Science* **9**: 1445.
- 454 **Honkaniemi J, Ojansuu R, Kasanen R, Heliövaara K. 2018.** Interaction of disturbance agents on Norway  
 455 spruce: A mechanistic model of bark beetle dynamics integrated in simulation framework  
 456 WINDROT. *Ecological Modelling* **388**: 45-60.
- 457 **Hoover DL, Wilcox KR, Young KE. 2018.** Experimental droughts with rainout shelters: a methodological  
 458 review. *Ecosphere* **9**: e02088.
- 459 **Huang J, Hartmann H, Hellén H, Wisthaler A, Perreca E, Weinhold A, Rucker A, van Dam NM,  
 460 Gershenson J, Trumbore SE, et al. 2018.** New perspectives on CO<sub>2</sub>, temperature and light effects  
 461 on BVOC emissions using online measurements by PTR-MS and cavity ring-down spectroscopy.  
 462 *Environmental Science & Technology* **52**: 13811–13823.
- 463 **Huang J, Hammerbacher A, Weinhold A, Reichelt M, Gleixner G, Behrendt T, van Dam NM, Sala A,  
 464 Gershenson J, Trumbore S, et al. 2019.** Eyes on the future – evidence for trade-offs between  
 465 growth, storage and defense in Norway spruce. *New Phytologist* **222**: 144-158.



- 466 **Jamieson MA, Trowbridge AM, Raffa KF, Lindroth RL. 2012.** Consequences of climate warming and  
 467 altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology*  
 468 **160**: 1719-1727.
- 469 **Jamieson MA, Burkle LA, Manson JS, Runyon JB, Trowbridge AM, Zientek J. 2017.** Global change effects  
 470 on plant–insect interactions: the role of phytochemistry. *Current Opinion in Insect Science* **23**:  
 471 70-80.
- 472 **Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B. 2012.** Guess the impact of *Ips*  
 473 *typographus*-An ecosystem modelling approach for simulating spruce bark beetle outbreaks.  
 474 *Agricultural and Forest Meteorology* **166**: 188-200.
- 475 **Joseph G, Kelsey RG, Peck RW, Niwa CG. 2001.** Response of some scolytids and their predators to  
 476 ethanol and 4-allylanisole in pine forests of central Oregon. *Journal of Chemical Ecology* **27**: 697-  
 477 715.
- 478 **Kandasamy D, Gershenzon J, Andersson MN, Hammerbacher A. 2019.** Volatile organic compounds  
 479 influence the interaction of the Eurasian spruce bark beetle (*Ips typographus*) with its fungal  
 480 symbionts. *The ISME Journal*. doi:10.1038/s41396-019-0390-3
- 481 **Kautz M, Schopf R, Imron MA. 2014.** Individual traits as drivers of spatial dispersal and infestation  
 482 patterns in a host–bark beetle system. *Ecological Modelling* **273**: 264-276.
- 483 **Kautz M, Meddens AJH, Hall RJ, Arneth A. 2017.** Biotic disturbances in Northern Hemisphere forests – a  
 484 synthesis of recent data, uncertainties and implications for forest monitoring and modelling.  
 485 *Global Ecology and Biogeography* **26**: 533-552.
- 486 **Kessler A. 2015.** The information landscape of plant constitutive and induced secondary metabolite  
 487 production. *Current Opinion in Insect Science* **8**: 47-53.
- 488 **Klutsch JG, Erbilgin N. 2018.** Dwarf mistletoe infection in jack pine alters growth–defense relationships.  
 489 *Tree Physiology* **38**: 1538-1547.
- 490 **Koricheva J, Larsson S, Haukioja E, Keinanen M. 1998.** Regulation of woody plant secondary metabolism  
 491 by resource availability: hypothesis testing by means of meta-analysis. *Oikos* **83**: 212-226.
- 492 **Landhausser SM, Chow PS, Dickman LT, Furze ME, Kuhlman I, Schmid S, Wiesenbauer J, Wild B,  
 493 Gleixner G, Hartmann H, et al. 2018.** Standardized protocols and procedures can precisely and  
 494 accurately quantify non-structural carbohydrates. *Tree Physiology* **38**: 1764-1778.
- 495 **Landry JS, Price DT, Ramankutty N, Parrott L, Matthews HD. 2016.** Implementation of a Marauding  
 496 Insect Module (MIM, version 1.0) in the Integrated Biosphere Simulator (IBIS, version 2.6b4)  
 497 dynamic vegetation-land surface model. *Geoscientific Model Development* **9**: 1243-1261.
- 498 **Le Roux X, Lacoite A, Escobar-Gutiérrez A, Le Dizès S. 2001.** Carbon-based models of individual tree  
 499 growth: A critical appraisal. *Annals of Forest Science* **58**: 469-506.
- 500 **Li W, Hartmann H, Adams HD, Zhang H, Jin C, Zhao C, Guan D, Wang A, Yuan F, Wu J. 2018.** The sweet  
 501 side of global change–dynamic responses of non-structural carbohydrates to drought, elevated  
 502 CO<sub>2</sub> and nitrogen fertilization in tree species. *Tree Physiology* **38**: 1706-1723.
- 503 **McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres  
 504 N, et al. 2013.** Evaluating theories of drought-induced vegetation mortality using a multimodel–  
 505 experiment framework. *New Phytologist* **200**: 304-321.
- 506 **Meddens AJH, Hicke JA, Ferguson CA. 2012.** Spatiotemporal patterns of observed bark beetle-caused  
 507 tree mortality in British Columbia and the western United States. *Ecological Applications* **22**:  
 508 1876-1891.
- 509 **Meddens AJH, Hicke JA, Macalady AK, Buotte PC, Cowles TR, Allen CD. 2015.** Patterns and causes of  
 510 observed piñon pine mortality in the southwestern United States. *New Phytologist* **206**: 91-97.
- 511 **Mithöfer A, Boland W. 2012.** Plant defense against herbivores: chemical aspects. *Annual Review of*  
 512 *Plant Biology* **63**: 431-450.
- 513 **Mooney HA. 1972.** The carbon balance of plants. *Annual Review of Ecology and Systematics* **3**: 315-346.

- 514 **Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer J, Rosner S,**  
515 **Kikuta S, Schume H, et al. 2015.** Do water-limiting conditions predispose Norway spruce to bark  
516 beetle attack? *New Phytologist* **205**: 1128-1141.
- 517 **Oliva J, Stenlid J, Martinez-Vilalta J. 2014.** The effect of fungal pathogens on the water and carbon  
518 economy of trees: implications for drought-induced mortality. *New Phytologist* **203**: 1028-1035.
- 519 **Raffa KF, Aukema B, Erbilgin N, Klepzig K, Wallin K 2005.** Interactions among conifer terpenoids and  
520 bark beetles across multiple levels of scale: an attempt to understand links between population  
521 patterns and physiological processes. In: Romeo JT ed. *Recent Advances in Phytochemistry*.  
522 Toronto, Canada: Elsevier, 79-118.
- 523 **Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008.** Cross-scale drivers  
524 of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle  
525 eruptions. *Bioscience* **58**: 501-517.
- 526 **Raffa KF. 2014.** Terpenes tell different tales at different scales: glimpses into the Chemical Ecology of  
527 conifer - bark beetle - microbial interactions. *Journal of Chemical Ecology* **40**: 1-20.
- 528 **Raffa KF, Mason CJ, Bonello P, Cook S, Erbilgin N, Keefover-Ring K, Klutsch JG, Villari C, Townsend PA.**  
529 **2017.** Defence syndromes in lodgepole – whitebark pine ecosystems relate to degree of  
530 historical exposure to mountain pine beetles. *Plant, Cell & Environment* **40**: 1791-1806.
- 531 **Robinson EA, Ryan GD, Newman JA. 2012.** A meta-analytical review of the effects of elevated CO<sub>2</sub> on  
532 plant-arthropod interactions highlights the importance of interacting environmental and  
533 biological variables. *New Phytologist* **194**: 321-336.
- 534 **Roth M, Hussain A, Cale JA, Erbilgin N. 2018.** Successful colonization of lodgepole pine trees by  
535 mountain pine beetle increased monoterpene production and exhausted carbohydrate reserves.  
536 *Journal of Chemical Ecology* **44**: 209-214.
- 537 **Running SW. 2008.** Ecosystem disturbance, carbon, and climate. *Science* **321**: 652-653.
- 538 **Ryan MG, Sapes G, Sala A, Hood SM. 2015.** Tree physiology and bark beetles. *New Phytologist* **205**: 955-  
539 957.
- 540 **Scheller RM, Kretchun AM, Loudermilk EL, Hurteau MD, Weisberg PJ, Skinner C. 2018.** Interactions  
541 among fuel management, species composition, bark beetles, and climate change and the  
542 potential effects on forests of the lake Tahoe Basin. *Ecosystems* **21**: 643-656.
- 543 **Schiebe C, Hammerbacher A, Birgersson G, Witzell J, Brodelius PE, Gershenson J, Hansson BS, Krokene**  
544 **P, Schlyter F. 2012.** Inducibility of chemical defenses in Norway spruce bark is correlated with  
545 unsuccessful mass attacks by the spruce bark beetle. *Oecologia* **170**: 183-198.
- 546 **Schroeder M, Lindelöw Å. 2003.** Response of *Ips typographus* (Scolytidae: Coleoptera) and other bark-  
547 and wood-boring beetles to a flash-flood event. *Scandinavian Journal of Forest Research* **18**:  
548 218-224.
- 549 **Seidl R, Fernandes PM, Fonseca TF, Gillet F, Jönsson AM, Merganičová K, Netherer S, Arpaci A,**  
550 **Bontemps J-D, Bugmann H, et al. 2011.** Modelling natural disturbances in forest ecosystems: a  
551 review. *Ecological Modelling* **222**: 903-924.
- 552 **Seidl R, Muller J, Hothorn T, Bassler C, Heurich M, Kautz M. 2016.** Small beetle, large-scale drivers: how  
553 regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of*  
554 *Applied Ecology* **53**: 530-540.
- 555 **Seidl R, Rammer W. 2017.** Climate change amplifies the interactions between wind and bark beetle  
556 disturbances in forest landscapes. *Landscape Ecology* **32**: 1485-1498.
- 557 **Senf C, Pflugmacher D, Zhiqiang Y, Sebald J, Knorn J, Neumann M, Hostert P, Seidl R. 2018.** Canopy  
558 mortality has doubled in Europe's temperate forests over the last three decades. *Nature*  
559 *Communications* **9**: 4978.
- 560 **Sevanto S. 2018.** Drought impacts on phloem transport. *Current Opinion in Plant Biology* **43**: 76-81.

- 561 **Simard M, Pinto N, Fisher JB, Baccini A. 2011.** Mapping forest canopy height globally with spaceborne  
562 lidar. *Journal of Geophysical Research: Biogeosciences* **116**: G04021.
- 563 **Sun JH, Lu M, Gillette NE, Wingfield MJ. 2013.** Red turpentine beetle: innocuous native becomes  
564 invasive tree killer in China. *Annual Review of Entomology* **58**: 293-311.
- 565 **Temperli C, Veblen TT, Hart SJ, Kulakowski D, Tepley AJ. 2015.** Interactions among spruce beetle  
566 disturbance, climate change and forest dynamics captured by a forest landscape model.  
567 *Ecosphere* **6**: art231.
- 568 **Trumbore S, Brando P, Hartmann H. 2015.** Forest health and global change. *Science* **349**: 814-818.
- 569 **Villari C, Faccoli M, Battisti A, Bonello P, Marini L. 2014.** Testing phenotypic trade-offs in the chemical  
570 defence strategy of Scots pine under growth-limiting field conditions. *Tree Physiology* **34**: 919-  
571 930.
- 572 **Weber R, Gessler A, Hoch G. 2019.** High carbon storage in carbon-limited trees. *New Phytologist* **222**:  
573 171-182.
- 574 **Wiley E, Rogers BJ, Hodgkinson R, Landhäusser SM. 2016.** Nonstructural carbohydrate dynamics of  
575 lodgepole pine dying from mountain pine beetle attack. *New Phytologist* **209**: 550-562.
- 576 **Zeneli G, Krokene P, Christiansen E, Krekling T, Gershenson J. 2006.** Methyl jasmonate treatment of  
577 mature Norway spruce (*Picea abies*) trees increases the accumulation of terpenoid resin  
578 components and protects against infection by *Ceratocystis polonica*, a bark beetle-associated  
579 fungus. *Tree Physiology* **26**: 977-988.
- 580 **Zhao T, Krokene P, Hu J, Christiansen E, Bjorklund N, Langstrom B, Solheim H, Borg-Karlson A-K. 2011.**  
581 Induced terpene accumulation in Norway spruce inhibits bark beetle colonization in a dose-  
582 dependent manner. *Plos One* **6**: e26649.
- 583 **Zhao T, Kandasamy D, Krokene P, Chen J, Gershenson J, Hammerbacher A. 2019.** Fungal associates of  
584 the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer  
585 phenolics and influence bark beetle tunneling behavior. *Fungal Ecology* **38**: 71-79.

586

587

588 **Tables**

589 Table 1 Major bark beetle species known to promote or cause significant mortality on conifers.  
 590 Categorization of life history strategy is based on physiological condition of trees beetles  
 591 commonly colonize, although this can vary with population phase (Raffa *et al.*, 1993). For an  
 592 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	<i>Dendroctonus frontalis</i>	<i>Pinus echinata</i> , <i>Pinus engelmannii</i> , <i>Pinus leiophylla</i> , <i>Pinus ponderosa</i> , <i>Pinus rigida</i> , <i>Pinus taeda</i> , <i>Pinus virginiana</i>	<i>Entomocorticium</i> sp. A, <i>Ceratocystiopsis ranaculosus</i>	Primary
Mountain Pine Beetle	<i>Dendroctonus ponderosae</i>	<i>Pinus contorta</i> , <i>Pinus ponderosa</i> , <i>Pinus albicaulis</i>	<i>Grosmannia clavigera</i> , <i>Ophiostoma montium</i> , <i>Leptographium longiclavatum</i> , <i>Entomocorticium dendroctoni</i>	Primary
North American Spruce beetle	<i>Dendroctonus rufipennis</i>	<i>Picea engelmannii</i> , <i>Picea glauca</i> , <i>Picea sitchensis</i>	<i>Leptographium abietinum</i> , <i>Endoconidiophora rufipenni</i>	Primary
Piñon Ips	<i>Ips confusus</i>	<i>Pinus edulis</i> , <i>Pinus monophylla</i>		Secondary
European Spruce Bark Beetle	<i>Ips typographus</i>	<i>Picea abies</i>	<i>Endoconidiophora polonica</i> , <i>Grosmannia penicillata</i> , <i>Grosmannia europhioides</i> , <i>Ophiostoma bicolor</i> , <i>Ophiostoma ainoae</i>	Primary

593

594

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

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

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

599

600 **Figure captions**

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

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

620 **Figure 3** Distribution of bark beetle infestation models (n = 34) across three variables: bark beetle  
621 genus, implemented defence mechanism, and model type (DGVM = dynamic global vegetation  
622 model, FLM = forest landscape model, ABM = agent-based model). For the full list of models and  
623 methodological details see Table S3 and Methods S2 in the Supplementary Information. Flow  
624 width represents the number of models for each block of the three variables that are assigned to  
625 vertically-arranged axes. Both level of process detail in defence mechanism (centred axis) and  
626 spatial scope of the model type (right axis) typically increase from bottom to top. Structural  
627 parameters (e.g. tree age or size) play a major role in simulated tree defence yet, while climate-

628 driven defence triggers (e.g. drought indices) are less frequent, and only one model explicitly  
629 accounts for tree physiology-based defence (NSC pool) against bark beetles.

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

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

645

646 **Supporting Information**

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

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

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

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

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

655