

Tree mortality from drought, insects, and their interactions in a changing climate

Journal:	<i>New Phytologist</i>
Manuscript ID:	NPH-R-2014-18785.R2
Manuscript Type:	R - Research Review
Date Submitted by the Author:	n/a
Complete List of Authors:	Anderegg, William; Princeton University, Princeton Environmental Institute; Carnegie Institution for Science, Department of Global Ecology Hicke, Jeff; University of Idaho, Department of Geography Fisher, Rosie; UCAR, Climate & Global Dynamics Allen, Craig; USGS, Bandelier National Monument Aukema, Juliann; National Center for Ecological Analysis and Synthesis, * Bentz, Barbara; USDA Forest Service, Rocky Mountain Research Station Hood, Sharon; University of Montana, Division of Biological Sciences Lichstein, Jeremy Macalady, Alison; University of Arizona, Laboratory of Tree-Ring Research McDowell, Nate; Los Alamos National Laboratory, Earth and Environmental Sciences Division; Pan, Yude; USDA Forest Service, Northern Research Station Raffa, Kenneth; University of Wisconsin - Madison, Entomology Sala, Anna; The University of Montana, Div. Biological Sciences; Shaw, John; USDA Forest Service, Rocky Mountain Research Station Stephenson, Nathan L; USGS, Western Ecological Research Center, Sequoia and Kings Canyon Field Station Tague, Christina; University of California Santa Barbara, Bren School of the Environment Zeppel, Melanie; Macquarie University, Biological Sciences
Key Words:	Plant defenses, Population dynamics, Biosphere-Atmosphere interactions, Carbon cycle, Growth differentiation balance hypothesis, Disturbance, Trophic interactions

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

Tree mortality from drought, insects, and their interactions in a changing climate

William R. L. Anderegg^{1*}, Jeffrey A. Hicke², Rosie A. Fisher³, Craig D. Allen⁴, Juliann Aukema⁵, Barbara Bentz⁶, Sharon Hood⁷, Jeremy W. Lichstein⁸, Alison K. Macalady⁹, Nate McDowell¹⁰, Yude Pan¹¹, Kenneth Raffa¹², Anna Sala⁷, John D. Shaw¹³, Nathan L. Stephenson¹⁴, Christina Tague¹⁵, Melanie Zeppel¹⁶

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton NJ 08540,

²Department of Geography, University of Idaho, Moscow, ID 83844, ³National Center for

Atmospheric Research, Boulder, Colorado, 80305., ⁴U.S. Geological Survey, Fort Collins

Science Center, Jemez Mountains Field Station, Los Alamos, NM 87544, ⁵National Center for

Ecological Analysis and Synthesis, Santa Barbara CA 93117, ⁶USDA Forest Service, Rocky

Mountain Research Station, Logan UT 84321, ⁷Division of Biological Sciences, The University

of Montana, Missoula, MT 59812, ⁸ Department of Biology, University of Florida, Gainesville,

FL 32611, ⁹School of Geography and Development, University of Arizona, Tucson, AZ 85712,

¹⁰Earth and Environmental Sciences Division, Los Alamos National Lab, Los Alamos, NM

87545, ¹¹Northern Research Station, U.S. Forest Service, Newtown Square, PA 19073,

¹²Department of Entomology, University of Wisconsin, Madison, WI 53706, ¹³Rocky Mountain

Research Station, U.S. Forest Service, Ogden, UT 84401, ¹⁴U.S. Geological Survey, Western

23 *Ecological Research Center, 47050 Generals Highway #4, Three Rivers, CA 93271, USA,*
24 ¹⁵*Bren School of Environmental Science and Management, University of California – Santa*
25 *Barbara, Santa Barbara CA 93106, ¹⁶Department of Biological Sciences, Macquarie University*
26 *NSW 2109, Australia*

27

28

29

30

31

32

33

34

35

36 Word counts

37 Summary: 161

38 Introduction: 709

39 Framework: 1132

40 Mortality pathways: 1103

41 Cross-biome patterns: 686

42 Tools and approaches: 1040

43 Conclusion: 294

44 Key words: Biosphere-atmosphere feedbacks, carbon cycle, dynamic global vegetation model,
45 disturbance, trophic interactions

Anderegg et al. – Manuscript – 2

46 *Summary*

47 Climate change is expected to drive increased tree mortality through drought, heat stress,
48 and insect attacks, with manifold impacts on forest ecosystems. Yet, climate-induced tree
49 mortality and biotic disturbance agents are largely absent from process-based ecosystem models.
50 Using data sets from western USA and associated studies, we present a framework for
51 determining the relative contribution of drought stress, insect attack, and their interactions, which
52 is critical for modeling mortality in future climates. We outline a simple approach that identifies
53 the mechanisms associated with two guilds of insects – bark beetles and defoliators – which are
54 responsible for substantial tree mortality. We then discuss cross-biome patterns of insect-driven
55 tree mortality and draw upon available evidence contrasting the prevalence of insect outbreaks in
56 temperate and tropical regions. We conclude with an overview of tools and promising avenues to
57 address major challenges. Ultimately, a multi-trophic approach that captures tree physiology,
58 insect populations, and tree-insect interactions will better inform projections of forest ecosystem
59 responses to climate change.

60

61

62

63

64

65

66

67

68

69 **Introduction**

70 Forests cover approximately 30% of the globe's land surface area, provide numerous
71 ecosystem services to human societies, and play a central role in global biogeochemical cycles
72 (Bonan, 2008). Yet the future of forest ecosystems given expected changes in climate and other
73 environmental drivers is uncertain. Warming and drought, sometimes co-occurring with insect
74 outbreaks, have been linked to tree mortality in many regions, and future changes in climate are
75 expected to drive more extensive, severe, or frequent tree mortality events (Allen *et al.*, 2010).
76 Forest mortality can have manifold consequences for biodiversity, ecosystem function and
77 services, and feedbacks to climate change through biophysical effects and loss of carbon sinks
78 (Adams *et al.*, 2010; Anderegg *et al.*, 2013). The mechanisms that lead to forest mortality are
79 complex and include plant physiological responses to climate, climate influences on insect pests
80 and pathogens, and their interactions. Efforts to model climate-driven forest mortality, however,
81 most often focus on tree physiological responses to drought (Tague *et al.*, 2013; Anderegg *et al.*,
82 2015) and, very rarely, on tree responses to insect attack (Dietze & Matthes, 2014), but no model
83 exists that incorporates both drought and insects and their interaction.

84 Approaches to model drought-induced tree or forest mortality typically define drought
85 from an ecosystem water use perspective using such measures as an extended period of above-
86 average climatic water deficit, i.e., unusually large or persistent excess of water demand by
87 evaporation and transpiration relative to supply. A rapidly evolving plant physiology literature
88 that examines tree responses to drought and how these can lead to tree mortality provides a basis
89 to incorporate the effects of drought on trees in models. Research on tree responses focus on
90 failure of the hydraulic system to conduct water (Anderegg *et al.*, 2012b; Nardini *et al.*, 2013;
91 Urli *et al.*, 2013) and reductions in available carbohydrates (e.g. O'Brien *et al.*, 2014).

92 Insect outbreaks are often driven by drought, which stresses host trees (Raffa *et al.*,
93 2008), but also by many other factors. Temperature directly affects insects through
94 developmental rates and survival that drive population success (Regniere and Bentz 2007;
95 Powell and Bentz 2009; Weed *et al.* 2013). Characteristics of host trees such as abundance,
96 density, size, and physiology, and their spatial pattern across the landscape, are known to
97 influence the capacity for insect population growth and spread (Raffa *et al.*, 2008). Community
98 associates (e.g., natural enemies and symbiotic associates) influence population outbreaks and
99 subsequent tree mortality and are also affected by climate (Hajek, 1999; Régnière & Nealis,
100 2007; Raffa *et al.*, 2008; Six, 2013). Clearly, the interaction of drought and insects may lead to
101 increased insect populations with disproportionate consequences on tree mortality that may not
102 be accounted for by drought or insects alone.

103 While mechanistic and conceptual models of insect population dynamics (Dietze &
104 Matthes, 2014; Powell & Bentz, 2014) and ecosystem carbon cycling in response to climate
105 (Fisher *et al.*, 2010; Powell *et al.*, 2013; Tague *et al.*, 2013) have been used to estimate forest
106 mortality, a key question is how well can models incorporate both the drought-induced tree
107 physiological responses as well as representation of the effects of insects outbreaks that respond
108 to both climate and host condition.

109 In this paper, we argue that an integrated approach that considers both drought and
110 insects is needed to accurately predict forest dynamics in a changing climate. We first present a
111 framework that provides conceptual models of drought, insects, and their interactions that can
112 serve as guides for implementing a fully coupled insect-drought physiology model of tree
113 mortality. We then briefly summarize the mechanisms by which plants respond physiologically
114 to drought. We further illustrate the mechanisms by which two major categories of insects, bark

115 beetles and defoliators, kill trees, and show the linkages between insects and drought. Our
116 framework suggests a continuum of forest mortality drivers, from mortality mostly dominated by
117 drought effects on tree physiology independent of insects to mortality dominated by insect
118 dynamics independent of drought. We highlight the measurements that might contribute to
119 identifying where on this spectrum a given mortality event occurs and identify events where both
120 insects and plant drought response must be considered. Finally, we review the evidence for
121 cross-biome patterns in the relative importance of insect- and drought-triggered mortality and
122 highlight promising avenues for future research.

123

124 **Partitioning the roles of drought, insects, and their interactions in recent tree mortality**

125 The coupling between drought and insect outbreaks in many past events suggests that a
126 simple approach for including the effects of insects might be based on drought metrics.

127 However, this approach is often overly simplistic. We posit that it is critical to separate and
128 understand the relative contribution of insects and drought tree responses when:

129 1) insect and tree physiology exhibit different responses to climate drivers; for instance,
130 winter warming is likely to have a disproportionate effect on overwintering insect
131 population dynamics (e.g. Bentz *et al.*, 2010) relative to their host trees;

132 2) non-linear thresholds can be passed where drought processes can favor initial insect
133 population increments but thereafter no longer drive tree mortality; for example,
134 populations of aggressive bark beetles rely on stressed trees at low beetle densities, but
135 at high beetle densities healthy trees are killed (Raffa *et al.*, 2008); or

136 3) interactions between insects and tree physiology lead to non-additive effects in tree
137 mortality rates; for example, moderate (but non-lethal) drought can make trees more

138 vulnerable to dying from defoliation (often non-lethal alone) or more susceptible to
139 subsequent lethal attack by wood borers, secondary bark beetles, and latent pathogens
140 (Davidson *et al.*, 1999; Wallin & Raffa, 2001; Muilenburg & Herms, 2012).

141 We show below that one or more of these three cases are met for multiple major mortality events
142 affecting millions of hectares of forest in western North America (e.g., *Pinus contorta* and *Pinus*
143 *edulis*). Partitioning of the relative contribution of insects and host drought is useful for
144 separating causalities from correlations and to understand and predict these large-scale mortality
145 events in a changing climate.

146 Although existing broad frameworks include drought, insects, and their interactions in
147 driving tree mortality (e.g. Manion 1981, McDowell et al. 2008), no general method for
148 attributing their relative importance in tree death exists thus far. We present a general two-axis
149 framework for attributing the relative roles of drought, insects, and their interactions. Our
150 framework revolves around two central questions. How many trees would have died in a given
151 mortality event *with drought but without insects*? Conversely, how many trees would have died
152 in a given mortality event *with insects but without drought*? This gives rise to two hypothetical
153 numbers of dead trees in a focal region. In practice, these quantities can be difficult to determine
154 but can be estimated from sensitivities observed in field experiments (e.g., Gaylord *et al.*, 2013;
155 Netherer *et al.*, 2015) or from empirical relationships derived from previous insect outbreaks or
156 mortality events (Chapman *et al.*, 2012; Creeden *et al.*, 2014). Then, based on inventory plots,
157 aerial surveys, or satellite remote sensing, the observed number of dead trees can be estimated.
158 By comparing the relative sizes of the insect-free and drought-free hypothetical cases and the
159 observed mortality rates, it should be possible to determine the relative influence of each stressor
160 on mortality rates.

161 Several techniques and lines of evidence have been used to determine where mortality
162 events fall along a continuum from where the dominant driver of mortality was climate stress on
163 the tree to where it was climate influences on insect populations. Post-mortem assessments of
164 trees that died using field plots or inventory networks provide the most basic pieces of
165 information – were dead trees attacked by insects based on evidence such as bore holes or resin
166 exudates and, if so, at what densities and by which insect species? Figure 1 presents such
167 information as collected by the U.S. Forest Inventory and Analysis plot network. This network
168 assigns a *proximate* mortality agent based on visible evidence (e.g. insect galleries, fire scars)
169 (Fig. 1), although drought-kill can be difficult to determine visually and is thus more uncertain
170 (Supplementary Material). System knowledge of the ecosystem from previous mortality events
171 can also be informative. Are the insect species known to be primary agents that kill trees outright
172 or secondary agents that typically require stressed trees to be lethal? For example, several major
173 die-offs were strongly associated with physiological impacts of drought stress on trees, such as
174 widespread juniper, oak, and pine mortality in Texas in 2011 with relatively few signs of insect
175 attack (Twidwell *et al.*, 2014). In recent widespread trembling aspen (*Populus tremuloides*)
176 mortality in the Rocky Mountains and boreal forest in Canada, all observed biotic agents for
177 aspen are considered to be secondary (Marchetti *et al.*, 2011) and up to 20% of dead ramets had
178 no signs of biotic attack (Anderegg *et al.*, 2012b), indicating a major role of drought. Finally,
179 spatial patterns of mortality in relation to drought stress patterns or insect outbreak and dispersal
180 patterns also provide insight to the dominant drivers of mortality. For example, high mortality at
181 lower elevations, south-facing slopes, and in regions of the highest drought stress all support a
182 prominent role of drought stress driving mortality – although improved conditions for tree-killing
183 insects and pathogens on these warmer sites might also affect these patterns. On the end of the

184 drought-insect continuum (Fig. 2), climate influences on insect populations may be the dominant
185 driver in other mortality events. For example, in aggressive bark beetles the combination of a)
186 warm temperatures that directly benefit beetle population success and b) a supply of susceptible,
187 nutritionally optimal host trees is often necessary to shift insect populations across the endemic
188 to epidemic threshold (Raffa *et al.*, 2008). Warming has also allowed mountain pine beetle's
189 northward expansion into Canadian jack pine (Cullingham *et al.*, 2011) and enhanced beetle
190 survival in western high-elevation pine forests (Bentz *et al.*, 2013), absent any major drought
191 effects (Fig. 2).

192 Drought and insect stresses may also interact and lead to compounding effects on
193 mortality (Fig 2). The timing of mortality relative to climate anomalies is a crucial piece of
194 information. For example, in lodgepole pine (*Pinus contorta*), the correlation with drought extent
195 and mortality illustrates an important role for drought stress (Chapman *et al.*, 2012; Hart *et al.*,
196 2013), but the mortality event continued long after the observed drought stress had abated (Raffa
197 *et al.*, 2008; Creeden *et al.*, 2014). This indicates that the presence of higher insect populations
198 prolonged the mortality event, and thus might be categorized as a situation with compounding
199 stress. Experimental evidence can also reveal when and where drought and insects interact. For
200 example, a manipulative drought experiment revealed that drought stress predisposed piñon pine
201 (*Pinus edulis*) trees to attack by piñon ips beetles (*Ips confusus*) (Gaylord *et al.*, 2013),
202 highlighting that drought-insect interactions were critical in this recent widespread mortality
203 event (Breshears *et al.*, 2005; Meddens *et al.*, 2015).

204 Thus, in recent tree mortality events in western North America we find examples of
205 drought-driven, insect-driven, and drought-insect-interaction-driven tree mortality (Fig. 2). This
206 brief survey illustrates the importance of understanding not just the role of plant physiological

207 stress but also the wider context of insect population dynamics and tree physiology pertaining to
208 insect attack when studying climate-induced tree mortality.

209

210 **Drought and insect mortality pathways**

211 *Overview*

212 Most vegetation models do not explicitly consider the effects of insects but instead
213 implicitly assume that the impact of insects on plant death is accounted for in the temporally and
214 spatially averaged ‘background’ mortality rate (McDowell *et al.*, 2011). Moving beyond this
215 assumption will require both theoretical and empirical advances, ideally operating in tandem. To
216 this end, Dietze & Matthes (2014) propose a theoretical framework for modeling drought-insect
217 interactions in trees. The framework examines the effects of different insect functional groups
218 via changes in leaf area, phloem flow, xylem flow, stem turnover, and root biomass (Dietze &
219 Matthes, 2014). This useful framework could be extended by including a limited set of additional
220 processes for different insect feeding guilds (Koricheva *et al.*, 1998). First, in addition to direct
221 effects of climate on tree hosts, it could incorporate a mechanistic description of insect
222 population dynamics as a function of climate (direct effects of climate on insects; Fig. 3).
223 Second, and most importantly, it could incorporate the interaction between insects and tree
224 physiology and their consequences on mortality (indirect additive effects; y-axis in Fig. 2). We
225 propose that such interaction may be modeled with a basic physiological framework of the
226 physiology of plant defense, such as the Growth-Differentiation Balance Hypothesis (GDBH; see
227 below) (Herms & Mattson, 1992).

228 We begin with a baseline pathway that attributes mortality solely to drought stress on tree
229 physiology. As discussed above and previously (McDowell *et al.*, 2011; Anderegg *et al.*, 2012a;

Anderegg *et al.* – Manuscript – 10

230 Sala *et al.*, 2012), changes in plant hydraulics and carbon metabolism likely mediate the
231 multitude of drought mortality pathways. In ecosystem models, whole-plant hydraulic
232 conductivity (K_p), the hydraulic conductance of water within plant xylem vessels from the root
233 surface to the stomata, has frequently been used to represent both reductions in productivity with
234 drought and hydraulic failure (Martínez-Vilalta *et al.*, 2002). This concept integrates the
235 combined effects of water availability on biomass allocation to conducting tissue, transpiration,
236 and inherent xylem hydraulic properties. Similarly, nonstructural carbohydrate reserves (NSC)
237 may provide a time-integrated measure of the carbon status of a plant (Tague *et al.*, 2013). K_p
238 and NSC, however are interdependent: changes in K_p will affect carbon assimilation, and NSCs
239 have been implicated in xylem repair (Salleo *et al.*, 2009; Secchi *et al.*, 2011; Trifilò *et al.*,
240 2014), as well as on overall plant hydraulic integrity (O'Brien *et al.*, 2014). Future research
241 should focus on the interaction between K_p and NSC to better understand their respective
242 influence on each other and the subsequent specific thresholds that lead to mortality. In addition
243 to capturing tree physiological status, these two variables allow incorporation of several
244 important interconnections between trees and insect populations, particularly through secondary
245 metabolites (Fig. 3a), although other interconnections may also be important.

246

247 *Bark beetles*

248 Climate, particularly temperature, directly influences bark beetle populations, and
249 therefore tree mortality, through various processes: 1) larval growth and development; 2)
250 phenological timing that affects the degree of synchrony of emergence and mass attack; and 3)
251 cold- and heat-induced insect mortality (Bentz *et al.*, 2010) (Fig. 3b). Climate also influences
252 development and growth of fungal associates that contribute to a successful attack and provide

253 vital nutrients to developing larvae (Addison *et al.*, 2014). These elements of the conceptual
254 model are distinct from tree vulnerability and thus apply even in situations without much
255 drought-related host tree stress. Beetle populations are indirectly influenced by climate via stress
256 to the host tree, most notably drought, mediated primarily by tree secondary metabolites (Fig.
257 3b). The likelihood of successful attack increases under drought when reduction of carbon
258 assimilation and water transport decreases the tree's capacity to produce NSC and mobilize
259 secondary metabolites for defense production (Raffa & Berryman, 1983; Safranyik & Carroll,
260 2006). Developing larvae feed in the phloem while beetle fungal associates colonize both the
261 xylem and the phloem; both decrease K_p , leading to eventual tree death (Reed *et al.*, 2014).

262

263 *Defoliators*

264 Similar processes occur with defoliator-induced tree mortality, yet important differences
265 exist. For spring-feeding defoliators, phenology (larval emergence) must be synchronized with
266 key physiological processes of host trees (e.g., bud burst) for optimal insect population growth
267 (van Asch & Visser, 2007). Phenological synchrony can be highly sensitive to temperature, with
268 insects and host plants sometimes responding to warming at different rates (Schwartzberg *et al.*,
269 2014). Defoliator consumption of leaves depends on leaf nutritional quality and palatability,
270 which are influenced by secondary metabolites and plant nutrient status (Fig. 3c) (Wallin &
271 Raffa, 2001). By reducing leaf biomass, defoliators reduce net primary production (NPP) and
272 NSC production. Unlike bark beetle attacks that typically kill trees quickly, severe defoliation
273 over multiple years is usually required to kill trees, particularly in deciduous species (van Asch
274 & Visser, 2007). Natural enemies, which generally have a larger limiting effect on defoliator
275 population dynamics than on bark beetles, are affected by temperature (especially predators and

276 parasites) and precipitation (especially entomopathogens) (Jamieson *et al.*, 2012; Reilly *et al.*,
277 2014).

278

279 *Linking insects and tree physiology through secondary metabolites*

280 Theories of plant defense postulate allocation trade-offs between defense and other plant
281 functions, shifts in allocation depending on abiotic resource availability (e.g., nutrients, water),
282 and host fitness implications depending on resource availability, rates of herbivory and the
283 competitive environment (Loomis, 1932; Lorio Jr., 1986; Bazzaz *et al.*, 1987; Berryman, 1988;
284 Herms & Mattson, 1992; Tuomi, 1992). The expanded Growth-Differentiation Balance
285 Hypothesis (GDBH) provides a useful framework to predict plant defenses. Because drought
286 slows growth before photosynthesis, moderate drought will increase secondary metabolites,
287 which includes defensive structures and compounds (Herms & Mattson, 1992). Empirical and
288 model-based tests of plant carbon balance during drought support GDBH predictions in some
289 systems (Koricheva *et al.*, 1998). However, changes in defenses due to nutrient availability, CO₂
290 enrichment, and temperature have been tested more rigorously than drought stress, and it appears
291 that the GDBH is less adept at predicting tree defense levels vis-à-vis drought, but adequate tests
292 of this are rare. Defense levels did not appear to conform to the predictions of the GDBH in one
293 study that used two levels of water availability (Hale *et al.*, 2005). Resin flow in *Pinus edulis*
294 across three experimental drought levels matched the pattern predicted by the GDBH, but the
295 hypothesis could not be tested because growth rate was not measured (Gaylord *et al.*, 2013).
296 Applicability of GDBH also varies among different groups of defense compounds (Koricheva *et*
297 *al.*, 1998) and between constitutive and inducible defenses (Lewinsohn *et al.*, 1993). Thus, the
298 GDBH may provide a useful mechanistic link for connecting climate stress and tree defenses

299 based on recently assimilated versus stored carbon levels, but more tests are needed.

300

301 **Cross-biome patterns in insects' roles in tree mortality**

302 How the mechanisms articulated in Fig. 3 operate in different biomes is uncertain. Given
303 the importance of insects as herbivores in tropical forests, a better understanding of drought-
304 insect interactions in tropical forests is likely crucial to more realistically represent global
305 biogeochemical dynamics because of the significant contribution of these forests to the global
306 carbon cycle – but most recent literature on insect outbreaks has focused on temperate forests.
307 How do the relative roles of insects and drought vary across ecosystems and across the globe?
308 Cross-biome patterns of the relative roles of insects versus drought in causing tree mortality are
309 hampered by available data in tropical forests, but some generalizations can be made across
310 biomes. Compared to the insect outbreaks in temperate forests previously described, tropical
311 outbreaks usually affect fewer trees, largely because tropical forests are more diverse in species
312 composition and most herbivores are limited to one or a few related tree genera (Dyer *et al.*,
313 2012). Thus, we hypothesize that the relative severity of climate-sensitive insect-caused
314 mortality should increase with latitude as tree species diversity declines and the number of host
315 trees increases. Insects at high latitudes are also predicted to have relatively greater fitness as
316 climate warms because they are currently living below their thermal optima, compared to insects
317 at low latitudes that currently live very close to their thermal optima and face greater extinction
318 risks (Deutsch *et al.*, 2008). Although tropical outbreaks are usually most severe in areas of
319 highest host tree density (Dyer *et al.*, 2012), they can still occur in diffusely distributed host
320 species that comprise 1% or less of trees in a forest (e.g., Wong *et al.*, 1990). Importantly,
321 generalized outbreaks also do sometimes occur, with several different insect species

Anderegg et al. – Manuscript – 14

322 simultaneously attacking a taxonomically diverse array of tree species (Van Bael *et al.*, 2004;
323 Dyer *et al.*, 2012).

324 Although our understanding of outbreaks in species-rich tropical forests is less than in the
325 temperate and boreal zones (Dyer *et al.*, 2012), available information hints at some important
326 contrasts between tropical and temperate forests. For example, although several species of
327 tropical bark beetles and wood borers are known to undergo outbreaks (Nair, 2007; Dyer *et al.*,
328 2012), most published information on tropical outbreaks focuses on defoliators. The dominance
329 of publications on defoliators may be a consequence of defoliator outbreaks being more common
330 or it may reflect a reporting bias due to easier detection of defoliator outbreaks.

331 Many outbreaks in tropical forests – at least of defoliators – appear to be triggered by
332 drought. However, outbreaks often occur during the rainy season immediately following the
333 drought, perhaps in response to post-drought leaf flushes or delayed post-drought recovery of the
334 outbreaking herbivores' enemies (predators, parasitoids, and pathogens; Coley, 1998; Van Bael
335 *et al.*, 2004). Tropical outbreaks may generally be shorter than temperate outbreaks (weeks or
336 months rather than years; e.g. Wong *et al.*, 1990; Van Bael *et al.*, 2004), perhaps due to rapid
337 top-down control by enemies (Van Bael *et al.*, 2004). Tropical outbreaks also might, on average,
338 be more spatially restricted than temperate outbreaks. For example, Van Bael *et al.* (2004)
339 reported localized outbreaks along the Pacific Coast of Panama following a drought, but found
340 no outbreaks among the same host species in moister interior forests. A few tropical outbreaks
341 have been documented as long-lived and spatially extensive, particularly when host-tree densities
342 are high. Nair (2007) summarized a century's worth of outbreaks of *Hoplocerambyx spinicornis*
343 (a cerambycid beetle) in one of its host trees in India and found that the largest outbreak spanned
344 more than six years and 500,000 ha, killing millions of trees.

345 Finally, the role of higher trophic levels as negative feedbacks that control insect
346 outbreaks appear to be more important in tropical forests than extratropical forests. Predicting the
347 effects of climatic changes in these systems will thus depend on improved understanding of
348 climatic effects on trophic cascades. For example, if climatic changes disrupt the synchronization
349 of top-down control of outbreaking insects by their enemies (Coley, 1998; Stireman *et al.*, 2005),
350 we might expect more frequent, extensive, generalized, and long-lasting outbreaks in the future.

351

352 **Tools and approaches for moving forward**

353 Multiple experimental, observational, and modeling approaches appear promising for
354 attributing tree mortality to drought, insects, and their interactions, though each approach has its
355 limitations. Factorial experiments that manipulate both drought and insects have good potential
356 to improve understanding of tree drought response, insect population dynamics, and tree-insect
357 interactions, but to date are rare and expensive. Rainfall exclusion experiments have been widely
358 used to impose drought stress on forest ecosystems (Beier *et al.*, 2012; Zeppel *et al.*, 2014) and
359 have in some cases induced mortality in concert with insect attacks (e.g., (Gaylord *et al.*, 2013;
360 Netherer *et al.*, 2015). Insecticide sprays or manipulated insect introductions can control for
361 insect attack on certain trees, and factorial drought experiments with and without insect attack
362 may be a useful tool to disentangle the relative roles and climatic underpinnings of tree stress and
363 insect attack in mortality (Raffa & Berryman, 1983; Netherer *et al.*, 2015).

364 Observational data that include both tree mortality and insect abundances or presence in
365 dying trees, especially across different locations and ecosystem scales over longer time-periods,
366 will help advance our understanding. A few data sets are available that cover landscape and
367 broader scales over multiple years (e.g. Shaw *et al.*, 2005; Meddens *et al.*, 2012) (Fig. 1).

368 Satellite remote sensing, particularly time series of imagery, can be especially useful when
369 accuracy is evaluated against other observations such as field data and when attribution of tree
370 mortality to a disturbance agent is identified (Hansen *et al.*, 2013; McDowell *et al.*, 2014).
371 Quantification of insect abundance along with tree mortality is a critical data gap, and would be
372 especially useful if collected in concert with large-scale forest inventory networks. Empirical
373 studies of the causes of tree mortality that consider multiple factors, including climate, stand
374 structure, soil characteristics, and insect populations, will be particularly valuable.

375 Mechanistic models exist that simulate the internal physiology of tree hydraulic and
376 carbon status (McDowell *et al.*, 2013; Powell *et al.*, 2013) but will likely require substantial
377 empirical calibration (Fisher *et al.*, 2010) to account for uncertainty in meteorology and soil
378 physical properties that affect plant water supply and therefore accurate representation of drought
379 (Lichstein *et al.*, 2014). We posit that better modeling of internal plant physiology, such as plant
380 hydraulics along with coupling to mechanistic insect dynamics models (Fig. 2), will improve
381 higher-scale modeling of mortality due to drought, insects, and their interactions. For example, a
382 hydrological model that incorporated a plant hydraulic threshold was able to predict spatial
383 patterns in drought-driven mortality of *Populus tremuloides* with 75% accuracy and was a large
384 improvement on prediction from soil moisture, precipitation, or temperature alone (Anderegg *et*
385 *al.*, 2015).

386 Mechanistic models have also incorporated insect outbreaks in several studies in different
387 ways (see Hicke *et al.*, 2012 for a review). One way is involves prescribing insect-caused tree
388 mortality to study effects on vegetation structure and function by bark beetles (e.g., Kurz *et al.*,
389 2008; Edburg *et al.*, 2011) and other feeding guilds (Hogg, 1999; Keith *et al.*, 2012). Sensitivity
390 studies are useful for identifying key processes missing from models, such as the inclusion of

391 snags that have a large effect on heterotrophic respiration fluxes (Edburg *et al.*, 2011). Studies
392 of past events document the impacts of insect outbreaks on vegetation dynamics, including
393 influences on carbon fluxes that may affect national policy (Kurz *et al.*, 2008), although adequate
394 information about the extent, severity, and duration of tree mortality is needed. Investigations
395 have illustrated the advantages of detailed tree-based models run at stand scales (Pfeifer *et al.*,
396 2011) as well as less detailed growth and yield models (Kurz *et al.*, 2008) or global land surface
397 models (Edburg *et al.*, 2011) that permit large-scale assessments and/or linkages to Earth system
398 models. Effects of future outbreaks can be assessed by prescribing the timing and severity of
399 these events using scenarios, which is particularly effective with defoliator outbreaks given their
400 cyclical nature (Dymond *et al.*, 2010; Hennigar & MacLean, 2010). A disadvantage of the
401 scenario approach is that any coupling with climate may be limited.

402 A second way of incorporating insect outbreaks in mechanistic vegetation models is by
403 developing and including a prognostic insect outbreak model. Insect models to predict the
404 probability, extent, and/or severity of tree mortality that incorporate climate variables to predict
405 insect-caused tree mortality have used a mix of temperature and precipitation variables (Jewett *et*
406 *al.*, 2011; Preisler *et al.*, 2012). More recent mechanistic insect models also include spatially
407 explicit host tree densities (Powell & Bentz, 2014) and fungal associates (Addison *et al.*, 2014).
408 Inclusion of insect models in vegetation models allow assessment of the level of ecological
409 understanding (when results are evaluated against historical events) as well as estimate impacts
410 of future climate change and management decisions. However, such studies are rare given the
411 state of knowledge. A notable exception is the inclusion of European spruce bark beetle (*Ips*
412 *typographus*) in LPJ-GUESS (Jönsson *et al.*, 2012). Thus, more detailed coupling of tree and

413 insect models and additional applications to case studies should be possible, at least in some
414 ecosystems, in the near future (Fig. 2).

415 A key decision is when and how best to model insect population dynamics. The status
416 quo approach for typical vegetation models is that insect-induced death is implicitly included in
417 background mortality rates, meaning insect-caused mortality is not constant, but rather often
418 aggregated in space and time and non-linear. One approach relies on the dominance of
419 temperature as a significant driver of insect life cycles, and information on temperature-
420 dependent development times in outbreaking insect populations which are well studied (e.g.
421 Powell & Bentz, 2009). These climate-driven insect population models can be coupled with
422 ecosystem models (Jönsson *et al.*, 2012). Further complexity can be added by considering
423 diffusion or spread, where the probability of infestation varies as a function of proximity to other
424 currently infested trees (Preisler *et al.*, 2012; Powell & Bentz, 2014). Advantages of spatially
425 modeling insect population dynamics include the capacity to incorporate density-dependent
426 factors and the potential to better capture spatial and temporal variation in tree mortality that
427 results from climate-driven insect population growth. Disadvantages include the need for
428 additional parameters and model complexity, the lack of scientific understanding for many
429 processes, and the possibility of introducing erratic and unpredictable model behavior due to
430 greater model complexity.

431

432 **Conclusion**

433 Advancing our understanding of drought, biotic disturbance agents, and their interactions
434 is critical to develop and apply models that predict future patterns of tree mortality in a changing
435 world. Recent developments in tree mortality research have separately focused on the

436 physiology of trees under stress and on insects as tree-killing agents, yet these processes are
437 linked. Insects play many critical roles in physiology, demography, and disturbance of forest
438 ecosystems, although they are often not explicitly included in ecosystem models used to make
439 predictions of vegetation change or carbon cycling under climate scenarios. Furthermore, insect
440 outbreaks are strongly influenced by climate (both warming and drought), and the role of
441 drought varies by insect species. An important first step in predicting future mortality is to
442 identify situations where considering both agents is necessary. We argue that a fully coupled
443 approach is needed when: 1) insect and tree physiology exhibit different responses to climate
444 drivers 2) nonlinear thresholds can be passed where drought processes may incite but not be
445 needed to continue tree mortality or 3) interactions between insects and tree physiology lead to
446 non-additive effects in tree mortality rates. We present examples of different types of events
447 throughout western North America, and argue that it will be essential to study mortality in other
448 biomes, particularly the tropics, to improve mortality modeling under climate change. Our
449 conceptual model that links internal tree physiology with insect feeding guilds offers a pathway
450 for modeling drought-induced tree mortality, insect outbreaks, and their interaction in a fully
451 coupled approach. The representation of insect diversity according to their functional interaction
452 with trees (feeding guilds) provides a useful way to focus effort on understanding plant-insect
453 interactions at large spatial and temporal scales, and provides a much-needed common point of
454 interaction for cross-disciplinary science.

455

456

457

458 **Acknowledgements:** We thank the National Center for Ecological Analysis and Synthesis
 459 (NCEAS) for the support to convene the working group from which this paper originated. We
 460 also acknowledge the support of the U.S. Geological Survey's Ecosystems and Climate and Land
 461 Use Change mission areas.

462

463

464

465

466

467 **References**

468 **Adams HD, Macalady AK, Breshears DD, Allen CD, Stephenson NL, Saleska SR, Huxman**
 469 **TE, others. 2010.** Climate-Induced Tree Mortality: Earth System Consequences. *Eos,*
 470 *Transactions American Geophysical Union* **91**: 153–154.

471 **Addison A, Powell JA, Bentz BJ, Six DL. 2014.** Integrating models to investigate critical
 472 phenological overlaps in complex ecological interactions: The mountain pine beetle-fungus
 473 symbiosis. *Journal of theoretical biology* **368**: 55-66.

474 **Addison A, Powell J, Six D, Moore M, Bentz B. 2013.** The role of temperature variability in
 475 stabilizing the mountain pine beetle-fungus mutualism. *Journal of Theoretical Biology* **335**: 40-
 476 50.

477 **Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M,**
 478 **Kitzberger T, Rigling A, Breshears DD, Hogg EH, et al. 2010.** A global overview of drought
 479 and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest*
 480 *Ecology and Management* **259**: 660–684.

481 **Anderegg WRL, Alan Flint, Huang, Cho-ying, Flint, Lorraine, Berry, Joseph, Davis,**
 482 **Frank, Sperry, John, Field, Christopher. 2015.** Tree mortality predicted from drought-induced
 483 vascular damage. *Nature Geoscience* doi:10.1038/ngeo2400.

484 **Anderegg WR, Anderegg LD, Berry JA, Field CB. 2014.** Loss of whole-tree hydraulic
 485 conductance during severe drought and multi-year forest die-off. *Oecologia* **175**: 11–23.

486 **Anderegg WRL, Berry JA, Field CB. 2012a.** Linking definitions, mechanisms, and modeling
 487 of drought-induced tree death. *Trends in Plant Science* **17**: 693–700.

- 488 **Anderegg WRL, Berry JA, Smith DD, Sperry JS, Anderegg LDL, Field CB. 2012b.** The
 489 roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings*
 490 *of the National Academy of Sciences, USA* **109**: 233–237.
- 491 **Anderegg WRL, Callaway E. 2012.** Infestation and hydraulic consequences of induced carbon
 492 starvation. *Plant Physiology* **159**: 1866–1874.
- 493 **Anderegg WRL, Kane JM, Anderegg LDL. 2013.** Consequences of widespread tree mortality
 494 triggered by drought and temperature stress. *Nature Climate Change* **3**: 30–36.
- 495 **Van Asch M, Visser ME. 2007.** Phenology of forest caterpillars and their host trees: the
 496 importance of synchrony. *Annual Reviews of Entomology*. **52**: 37–55.
- 497 **Van Bael SA, Aiello A, Valderrama A, Medianero E, Samaniego M, Wright SJ. 2004.**
 498 General herbivore outbreak following an El Niño-related drought in a lowland Panamanian
 499 forest. *Journal of Tropical Ecology* **20**: 625–633.
- 500 **Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF. 1987.** Allocating Resources to Reproduction
 501 and Defense. *BioScience* **37**: 58–67.
- 502 **Beier C, Beierkuhnlein C, Wohlgemuth T, Penuelas J, Emmett B, Körner C, Boeck H,**
 503 **Christensen JH, Leuzinger S, Janssens IA. 2012.** Precipitation manipulation experiments–
 504 challenges and recommendations for the future. *Ecology Letters* **15**: 899–911.
- 505 **Bentz BJ, Logan JA, Amman GD. 1991.** Temperature-dependent development of the mountain
 506 pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *The Canadian*
 507 *Entomologist* **123**: 1083–1094.
- 508 **Bentz B, Mullins D. 1999.** Ecology of mountain pine beetle (Coleoptera: Scolytidae) cold
 509 hardening in the intermountain west. *Environmental Entomology* **28**: 577–587.
- 510 **Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF,**
 511 **Seybold SJ. 2010.** Climate Change and Bark Beetles of the Western United States and Canada:
 512 Direct and Indirect Effects. *BioScience* **60**: 602–613.
- 513 **Bentz B, Vandygriff J, Jensen C, Coleman T, Maloney P, Smith S, Grady A, Schen-**
 514 **Langenheilm G. 2013.** Mountain pine beetle voltinism and life history characteristics across
 515 latitudinal and elevational gradients in the western United States. *Forest Science* **60**: 000–000.
- 516 **Berryman AA. 1988.** Towards a Unified Theory of Plant Defense. In: Mattson WJ, Levieux J,
 517 Bernard-Dagan C, eds. Mechanisms of Woody Plant Defenses Against Insects. Springer New
 518 York, 39–55.
- 519 **Bonan GB. 2008.** Forests and climate change: Forcings, feedbacks, and the climate benefits of
 520 forests. *Science* **320**: 1444–1449.

- 521 **Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens**
522 **JH, Floyd ML, Belnap J, et al. 2005.** Regional vegetation die-off in response to global-change-
523 type drought. *Proceedings of the National Academy of Sciences, USA* **102**: 15144–15148.
- 524 **Chapman TB, Veblen TT, Schoennagel T. 2012.** Spatiotemporal patterns of mountain pine
525 beetle activity in the southern Rocky Mountains. *Ecology* **93**: 2175–2185.
- 526 **Coley PD. 1998.** Possible effects of climate change on plant/herbivore interactions in moist
527 tropical forests. *Climatic Change* **39**: 455–472.
- 528 **Creeden EP, Hicke JA, Buotte PC. 2014.** Climate, weather, and recent mountain pine beetle
529 outbreaks in the western United States. *Forest Ecology and Management* **312**: 239–251.
- 530 **Cullingham CI, Cooke JE, Dang S, Davis CS, Cooke BJ, Coltman DW. 2011.** Mountain pine
531 beetle host-range expansion threatens the boreal forest. *Molecular Ecology* **20**: 0.
- 532 **Davidson CB, Gottschalk KW, Johnson JE. 1999.** Tree mortality following defoliation by the
533 European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *Forest Science* **45**:
534 74–84.
- 535 **Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR.**
536 **2008.** Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the*
537 *National Academy of Sciences, USA* **105**: 6668–6672.
- 538 **Dietze MC, Matthes JH. 2014.** A general ecophysiological framework for modelling the impact
539 of pests and pathogens on forest ecosystems. *Ecology Letters* **17**: 1418–1426.
- 540 **Dyer LA, Carson WP, Leigh Jr EG. 2012.** Insect Outbreaks in Tropical Forests: Patterns,
541 Mechanisms, and Consequences. *Insect Outbreaks Revisited* **10**: 219–245.
- 542 **Dymond CC, Neilson ET, Stinson G, Porter K, MacLean DA, Gray DR, Campagna M,**
543 **Kurz WA. 2010.** Future spruce budworm outbreak may create a carbon source in eastern
544 Canadian forests. *Ecosystems* **13**: 917–931.
- 545 **Edburg SL, Hicke JA, Lawrence DM, Thornton PE. 2011.** Simulating coupled carbon and
546 nitrogen dynamics following mountain pine beetle outbreaks in the western United States.
547 *Journal of Geophysical Research (Biogeosciences)* **116**: 4033.
- 548 **Fisher R, McDowell N, Purves D, Moorcroft P, Sitch S, Cox P, Huntingford C, Meir P, Ian**
549 **Woodward F. 2010.** Assessing uncertainties in a second-generation dynamic vegetation model
550 caused by ecological scale limitations. *New Phytologist* **187**: 666–681.
- 551 **Frank JM, Massman WJ, Ewers BE, Huckaby LS, Negrón JF. 2014.** Ecosystem CO₂/H₂O
552 fluxes are explained by hydraulically limited gas exchange during tree mortality from spruce
553 bark beetles. *Journal of Geophysical Research: Biogeosciences* **119**: 1195–1215.

- 554 **Gaylord ML, Kolb TE, Pockman WT, Plaut JA, Yopez EA, Macalady AK, Pangle RE,**
 555 **McDowell NG. 2013.** Drought predisposes piñon–juniper woodlands to insect attacks and
 556 mortality. *New Phytologist* **198**: 567–578.
- 557 **Goodsman DW, Lusebrink I, Landhäuser SM, Erbilgin N, Lieffers VJ. 2013.** Variation in
 558 carbon availability, defense chemistry and susceptibility to fungal invasion along the stems of
 559 mature trees. *New Phytologist* **197**: 586–594.
- 560 **Hajek A. 1999.** Pathology and epizootiology of the Lepidoptera-specific mycopathogen
 561 *Entomophaga maimaiga*. *Microbiology and Molecular Biology Reviews* **63**: 814–835.
- 562 **Hale BK, Herms DA, Hansen RC, Clausen TP, Arnold D. 2005.** Effects of drought stress and
 563 nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance
 564 of poplar to two lymantriid defoliators. *Journal of Chemical Ecology* **31**: 2601–2620.
- 565 **Hansen EM, Bentz BJ, Turner DL. 2001.** Temperature-based model for predicting univoltine
 566 brood proportions in spruce beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* **133**:
 567 827–841.
- 568 **Hansen M, Potapov P, Moore R, Hancher M, Turubanova S, Tyukavina A, Thau D,**
 569 **Stehman S, Goetz S, Loveland T. 2013.** High-resolution global maps of 21st-century forest
 570 cover change. *Science* **342**: 850–853.
- 571 **Hart SJ, Veblen TT, Eisenhart KS, Jarvis D, Kulakowski D. 2013.** Drought induces spruce
 572 beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* **95**: 930–939.
- 573 **Hennigar CR, MacLean DA. 2010.** Spruce budworm and management effects on forest and
 574 wood product carbon for an intensively managed forest. *Canadian Journal of Forest Research*
 575 **40**: 1736–1750.
- 576 **Herms DA, Mattson WJ. 1992.** The dilemma of plants: To grow or defend. *The Quarterly*
 577 *Review of Biology* **67**: 283–335.
- 578 **Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Kashian DM, Moore D, Raffa KF,**
 579 **Sturrock RN, Vogelmann J. 2012.** Effects of biotic disturbances on forest carbon cycling in the
 580 United States and Canada. *Global Change Biology* **18**: 7–34.
- 581 **Hogg EH. 1999.** Simulation of interannual responses of trembling aspen stands to climatic
 582 variation and insect defoliation in western Canada. *Ecological Modelling* **114**: 175–193.
- 583 **Jamieson MA, Trowbridge AM, Raffa KF, Lindroth RL. 2012.** Consequences of climate
 584 warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant*
 585 *Physiology* **160**: 1719–1727.
- 586 **Jewett JT, Lawrence RL, Marshall LA, Gessler PE, Powell SL, Savage SL. 2011.**
 587 Spatiotemporal relationships between climate and whitebark pine mortality in the Greater
 588 Yellowstone Ecosystem. *Forest Science* **57**: 320–335.

- 589 **Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B. 2012.** Guess the impact
590 of *Ips typographus*—An ecosystem modelling approach for simulating spruce bark beetle
591 outbreaks. *Agricultural and Forest Meteorology* **166**: 188–200.
- 592 **Keith H, Van Gorsel E, Jacobsen KL, Cleugh HA. 2012.** Dynamics of carbon exchange in a
593 Eucalyptus forest in response to interacting disturbance factors. *Agricultural and Forest*
594 *Meteorology* **153**: 67–81.
- 595 **Koricheva J, Larsson S, Haukioja E, Keinänen M. 1998.** Regulation of woody plant
596 secondary metabolism by resource availability: hypothesis testing by means of meta-analysis.
597 *Oikos* **160**: 212–226.
- 598 **Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T,**
599 **Safranyik L. 2008.** Mountain pine beetle and forest carbon feedback to climate change. *Nature*
600 **452**: 987–990.
- 601 **Lewinsohn E, Gijzen M, Muzika RM, Barton K, Croteau R. 1993.** Oleoresinosis in Grand Fir
602 (*Abies grandis*) saplings and mature trees (modulation of this wound response by light and water
603 stresses). *Plant Physiology* **101**: 1021–1028.
- 604 **Lichstein JW, Golaz N-Z, Malyshev S, Shevliakova E, Zhang T, Sheffield J, Birdsey RA,**
605 **Sarmiento JL, Pacala SW. 2014.** Confronting terrestrial biosphere models with forest inventory
606 data. *Ecological Applications* **24**: 699–715.
- 607 **Lindroth RL. 2010.** Impacts of elevated atmospheric CO₂ and O₃ on forests: phytochemistry,
608 trophic interactions, and ecosystem dynamics. *Journal of Chemical Ecology* **36**: 2–21.
- 609 **Logan JA, Powell JA. 2001.** Ghost forests, global warming, and the mountain pine beetle
610 (Coleoptera: Scolytidae). *American Entomologist* **47**: 160.
- 611 **Loomis WE. 1932.** Growth-differentiation balance vs. carbohydrate-nitrogen ratio. *Proceedings*
612 *of the American Society of Horticultural Sciences* **29**: 240–245.
- 613 **Lorio Jr. PL. 1986.** Growth-differentiation balance: A basis for understanding southern pine
614 beetle-tree interactions. *Forest Ecology and Management* **14**: 259–273.
- 615 **Marchetti SB, Worrall JJ, Eager T. 2011.** Secondary insects and diseases contribute to sudden
616 aspen decline in southwestern Colorado, USA. *Canadian Journal of Forest Research-Revue*
617 *Canadienne De Recherche Forestiere* **41**: 2315–2325.
- 618 **Martínez-Vilalta J, Piñol J, Beven K. 2002.** A hydraulic model to predict drought-induced
619 mortality in woody plants: an application to climate change in the Mediterranean. *Ecological*
620 *Modelling* **155**: 127–147.
- 621 **McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011.** The
622 interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in*
623 *Ecology & Evolution* **26**: 523–532.

- 624 **McDowell NG, Coops NC, Beck PS, Chambers JQ, Gangodagamage C, Hicke JA, Huang**
 625 **C, Kennedy R, Krofcheck DJ, Litvak M, et al. 2014.** Global satellite monitoring of climate-
 626 induced vegetation disturbances. *Trends in Plant Science* **20**: 114-123.
- 627 **McDowell NG, Fisher RA, Xu C, Domec J, Hölttä T, Mackay DS, Sperry JS, Boutz A,**
 628 **Dickman L, Gehres N. 2013.** Evaluating theories of drought-induced vegetation mortality
 629 using a multimodel–experiment framework. *New Phytologist* **200**: 304–321.
- 630 **Meddens AJ, Hicke JA, Ferguson CA. 2012.** Spatiotemporal patterns of observed bark beetle-
 631 caused tree mortality in British Columbia and the western United States. *Ecological Applications*
 632 **22**: 1876–1891.
- 633 **Meddens AJ, Hicke JA, Macalady AK, Buotte PC, Cowles TR, Allen CD. 2015.** Patterns and
 634 causes of observed piñon pine mortality in the southwestern United States. *New Phytologist* **206**:
 635 91-97.
- 636 **Muilenburg VL, Herms DA. 2012.** A review of bronze birch borer (Coleoptera: Buprestidae)
 637 life history, ecology, and management. *Environmental Entomology* **41**: 1372–1385.
- 638 **Nair KS. 2007.** *Tropical forest insect pests: ecology, impact, and management.* Cambridge
 639 University Press, Cambridge, UK.
- 640 **Nardini A, Battistuzzo M, Savi T. 2013.** Shoot desiccation and hydraulic failure in temperate
 641 woody angiosperms during an extreme summer drought. *New Phytologist* **200**: 322-329.
- 642 **Netherer S, Matthews B, Katzensteiner K, Blackwell E, Henschke P, Hietz P, Pennerstorfer**
 643 **J, Rosner S, Kikuta S, Schume H, et al. 2015.** Do water-limiting conditions predispose Norway
 644 spruce to bark beetle attack? *The New Phytologist* **205**: 1128–1141.
- 645 **O’Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014.** Drought survival of tropical
 646 tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* **4**: 710–
 647 714.
- 648 **Paine T, Raffa K, Harrington T. 1997.** Interactions among scolytid bark beetles, their
 649 associated fungi, and live host conifers. *Annual Reviews of Entomology* **42**: 179–206.
- 650 **Pfeifer EM, Hicke JA, Meddens AJ. 2011.** Observations and modeling of aboveground tree
 651 carbon stocks and fluxes following a bark beetle outbreak in the western United States. *Global*
 652 *Change Biology* **17**: 339–350.
- 653 **Powell JA, Bentz BJ. 2009.** Connecting phenological predictions with population growth rates
 654 for mountain pine beetle, an outbreak insect. *Landscape Ecology* **24**: 657–672.
- 655 **Powell JA, Bentz BJ. 2014.** Phenology and density-dependent dispersal predict patterns of
 656 mountain pine beetle (*Dendroctonus ponderosae*) impact. *Ecological Modelling* **273**: 173–185.

- 657 **Powell TL, Galbraith DR, Christoffersen BO, Harper A, Imbuzeiro H, Rowland L,**
658 **Almeida S, Brando PM, Costa ACL, Costa MH. 2013.** Confronting model predictions of
659 carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New*
660 *Phytologist* **200**: 350–365.
- 661 **Preisler HK, Hicke JA, Ager AA, Hayes JL. 2012.** Climate and weather influences on spatial
662 temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* **93**:
663 2421–2434.
- 664 **Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008.**
665 Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics
666 of bark beetle eruptions. *BioScience* **58**: 501–517.
- 667 **Raffa K, Berryman A. 1983.** The role of host plant resistance in the colonization behavior and
668 ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* **79**: 27–49.
- 669 **Reed DE, Ewers BE, Pendall E. 2014.** Impact of mountain pine beetle induced mortality on
670 forest carbon and water fluxes. *Environmental Research Letters* **9**: 105004-105008.
- 671 **Régnière J, Nealis V. 2007.** Ecological mechanisms of population change during outbreaks of
672 the spruce budworm. *Ecological Entomology* **32**: 461–477.
- 673 **Reilly JR, Hajek AE, Liebhold AM, Plymale R. 2014.** Impact of *Entomophaga maimaiga*
674 (Entomophthorales: Entomophthoraceae) on Outbreak Gypsy Moth Populations (Lepidoptera:
675 Erebiidae): The Role of Weather. *Environmental entomology* **43**: 632–641.
- 676 **Safranyik L, Carroll AL. 2006.** The biology and epidemiology of the mountain pine beetle in
677 lodgepole pine forests. In: Safranyik L, Wilson WR, eds. The mountain pine beetle: a synthesis
678 of biology, management, and impacts on lodgepole pine. Victoria, British Columbia: Natural
679 Resources Canada, Canadian Forest Service, Pacific Forestry Centre, 3–66.
- 680 **Sala A, Woodruff DR, Meinzer FC. 2012.** Carbon dynamics in trees: feast or famine? *Tree*
681 *Physiology* **32**: 764–775.
- 682 **Salleo S, Trifilò P, Esposito S, Nardini A, Gullo MAL. 2009.** Starch-to-sugar conversion in
683 wood parenchyma of field-growing *Laurus nobilis* plants: a component of the signal pathway for
684 embolism repair? *Functional Plant Biology* **36**: 815–825.
- 685 **Schwartzberg EG, Jamieson MA, Raffa KF, Reich PB, Montgomery RA, Lindroth RL.**
686 **2014.** Simulated climate warming alters phenological synchrony between an outbreak insect
687 herbivore and host trees. *Oecologia* **175**: 1041–1049.
- 688 **Secchi F, Gilbert ME, Zwieniecki MA. 2011.** Transcriptome response to embolism formation
689 in stems of *Populus trichocarpa* provides insight into signaling and the biology of refilling. *Plant*
690 *Physiology* **157**: 1419–1429.

- 691 **Sevanto S, McDowell NG, Dickman LT, Pangle R, POCKMAN WT. 2013.** How do trees
 692 die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant, Cell & Environment*
 693 **37**: 153-161.
- 694 **Shaw JD, Steed BE, DeBlander LT. 2005.** Forest Inventory and Analysis (FIA) Annual
 695 Inventory Answers the Question: What Is Happening to Pinyon-Juniper Woodlands? *Journal of*
 696 *Forestry* **103**: 280–285.
- 697 **Six DL. 2013.** The bark beetle holobiont: why microbes matter. *Journal of Chemical Ecology*
 698 **39**: 989–1002.
- 699 **Stireman J, Dyer L, Janzen D, Singer M, Lill J, Marquis R, Ricklefs R, Gentry G,**
 700 **Hallwachs W, Coley P. 2005.** Climatic unpredictability and parasitism of caterpillars:
 701 implications of global warming. *Proceedings of the National Academy of Sciences, USA* **102**:
 702 17384–17387.
- 703 **Tague CL, McDowell NG, Allen CD. 2013.** An integrated model of environmental effects on
 704 growth, carbohydrate balance, and mortality of *Pinus ponderosa* forests in the southern Rocky
 705 Mountains. *PloS one* **8**: e80286.
- 706 **Thomson AJ, Shepherd RF, Harris JWE, Silversides RH. 1984.** Relating weather to
 707 outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera, Tortricidae), in
 708 British Columbia. *Canadian Entomologist* **116**: 375–381.
- 709 **Trifilò P, Barbera PM, Raimondo F, Nardini A, Gullo MAL. 2014.** Coping with drought-
 710 induced xylem cavitation: coordination of embolism repair and ionic effects in three
 711 Mediterranean evergreens. *Tree Physiology* **34**: 109–122.
- 712 **Tuomi J. 1992.** Toward integration of plant defence theories. *Trends in Ecology & Evolution* **7**:
 713 365–367.
- 714 **Twidwell D, Wonkka CL, Taylor CA, Zou CB, Twidwell JJ, Rogers WE. 2014.** Drought-
 715 induced woody plant mortality in an encroached semi-arid savanna depends on topoedaphic
 716 factors and land management. *Applied Vegetation Science* **17**: 42–52.
- 717 **Ungerer MJ, Ayres MP, Lombardero MJ. 1999.** Climate and the northern distribution limits
 718 of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography* **26**:
 719 1133–1145.
- 720 **Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013.** Xylem embolism
 721 threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology* **33**: 672–683.
- 722 **Wagner MR, Benjamin DM, Clancy KM, Schuh BA. 1983.** Influence of diterpene resin acids
 723 on feeding and growth of larch sawfly, *Pristiphora erichsonii* (Hartig). *Journal of Chemical*
 724 *Ecology* **9**: 119–127.

725 **Wallin KF, Raffa KF. 2001.** Effects of folivory on subcortical plant defenses: can defense
726 theories predict interguild processes? *Ecology* **82**: 1387–1400.

727 **Wong M, Wright SJ, Hubbell SP, Foster RB. 1990.** The spatial pattern and reproductive
728 consequences of outbreak defoliation in *Quararibea asterolepis*, a tropical tree. *The Journal of*
729 *Ecology*: 579–588.

730 **Wright L, Berryman A, Gurusiddaiah S. 1979.** Host resistance to the fir engraver beetle,
731 *Scolytus ventralis* (Coleoptera: Scolytidae): 4. Effect of defoliation on wound monoterpene and
732 inner bark carbohydrate concentrations. *The Canadian Entomologist* **111**: 1255–1262.

733 **Zeppel MJB, Wilks JV, Lewis JD. 2014.** Impacts of extreme precipitation and seasonal
734 changes in precipitation on plants. *Biogeosciences* **11**: 3083–3093.

735
736
737
738
739
740
741
742
743
744
745
746
747
748
749
750
751
752

753 Figure Legends

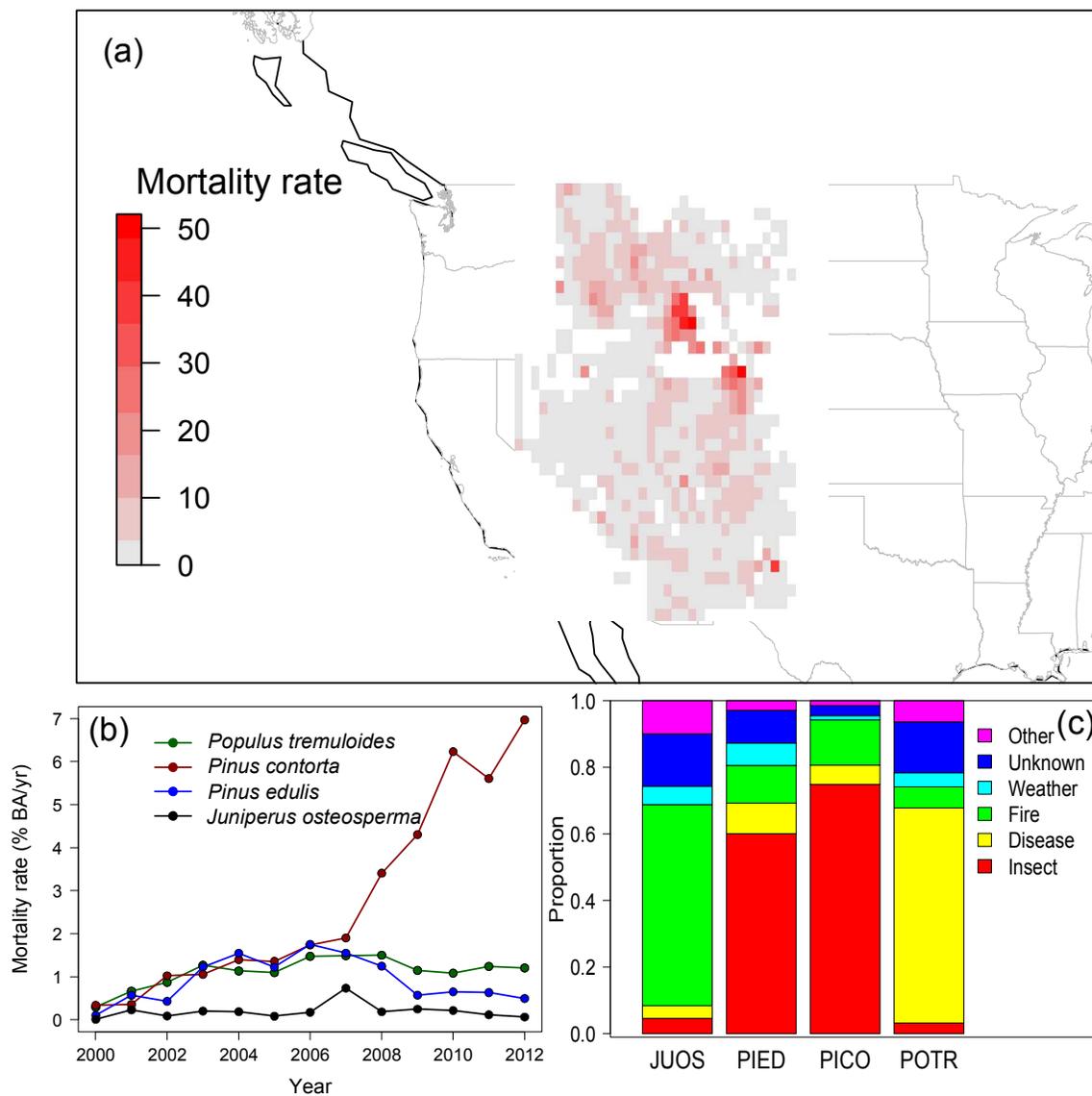
754 Figure 1: (a) Cumulative mortality rates (% Basal Area) of western US forests averaged over
 755 2000-2013, with fire-caused mortality removed from U.S. Forest Service Forest Inventory and
 756 Analysis data. (b) Annual mortality rates (% Basal Area/yr) of major tree species in the western
 757 United States from U.S. Forest Service Forest Inventory and Analysis data. (c) Field-ascribed
 758 proximate cause of mortality that crews noted about individual dead trees in *Juniperus*
 759 *osteosperma* (JUOS), *Pinus edulis* (PIED), *Pinus contorta* (PICO) and *Populus tremuloides*
 760 (POTR) (Supplemental Materials).

761
 762 Figure 2: Example attribution of the relative roles of drought stress, insect attack, and their
 763 interactions in recent angiosperm (orange) and gymnosperm (blue) mortality events in western
 764 North America. References for episodes: *Juniperus ashei* mortality in Texas (Twidwell et al.
 765 2014); *Populus tremuloides* mortality (Worrall et al. 2008; Anderegg et al. 2012; 2013; Worrall
 766 et al. 2013); *Pinus edulis* mortality (Breshears et al. 2005; Gaylord et al. 2013; Meddens et al.
 767 2015); *Pinus contorta* mortality (Chapman et al. 2012); *Pinus albicaulis* mortality (Bentz et al.
 768 2013).

769
 770 Figure 3: Conceptual framework of tree interactions with two insect guilds, illustrating tree
 771 mortality caused by climate and insects. Drought-induced tree mortality (a) occurs when climate
 772 variables influence net primary productivity (NPP) and plant hydraulic conductivity (K_p), which
 773 are interlinked with non-structural carbohydrate reserves (NSC) and biomass. In (b) and (c),
 774 insect feeding guilds of bark beetles and defoliators, respectively, are coupled with the tree
 775 model (green box) to lead to mortality. Thick black lines indicate pathways of tree mortality. In
 776 insect feeding guilds, dashed black lines indicate common links in both bark beetles and
 777 defoliators; solid black lines indicate differences between bark beetles and defoliators. Example
 778 references for process arrows: (1) (McDowell et al., 2011; Anderegg et al., 2014); (2)
 779 (McDowell et al., 2011; Anderegg & Callaway, 2012); (3) (Anderegg et al., 2012b; Sevanto et
 780 al., 2013; O'Brien et al., 2014); (4) (Safranyik & Carroll, 2006; Gaylord et al., 2013); (5)
 781 (Goodsman et al., 2013); (6) (Wright et al., 1979; Koricheva et al., 1998); (7) (Urli et al., 2013;
 782 Frank et al., 2014); (8) (Bentz et al., 2013); (9) (Bentz et al., 1991; Hansen et al., 2001); (10)
 783 (Paine et al., 1997; Addison et al., 2013); (11) (Paine et al., 1997; Safranyik & Carroll, 2006);
 784 (12) (Bentz & Mullins, 1999; Ungerer et al., 1999); (13) (Safranyik & Carroll, 2006); (14)
 785 (Safranyik & Carroll, 2006; Six, 2013); (15) (Raffa & Berryman, 1983; Safranyik & Carroll,
 786 2006); (16) (Logan & Powell, 2001); (17) (Bentz et al., 2010); (18) (Raffa & Berryman, 1983;
 787 Safranyik & Carroll, 2006); (19) (Thomson et al., 1984; Bentz et al., 2013); (20) (Thomson et
 788 al., 1984); (21) (Wagner et al., 1983; Lindroth, 2010); (22) (Thomson et al., 1984; Bentz et al.,
 789 2013).

790 **Figures**

791 Figure 1: (a) Cumulative mortality rates (% Basal Area) of western US forests averaged over
 792 2000-2013, with fire-caused mortality removed from U.S. Forest Service Forest Inventory and
 793 Analysis data. (b) Annual mortality rates (% Basal Area/yr) of major tree species in the western
 794 United States from U.S. Forest Service Forest Inventory and Analysis data. (c) Field-ascribed
 795 proximate cause of mortality that crews noted about individual dead trees in *Juniperus*
 796 *osteosperma* (JUOS), *Pinus edulis* (PIED), *Pinus contorta* (PICO) and *Populus tremuloides*
 797 (POTR) (Supplemental Materials).

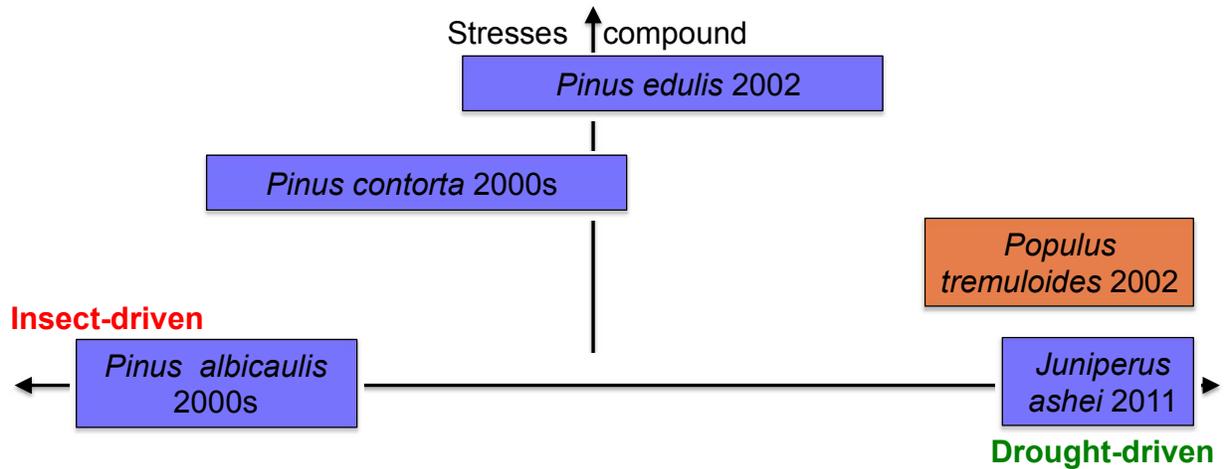


798

799

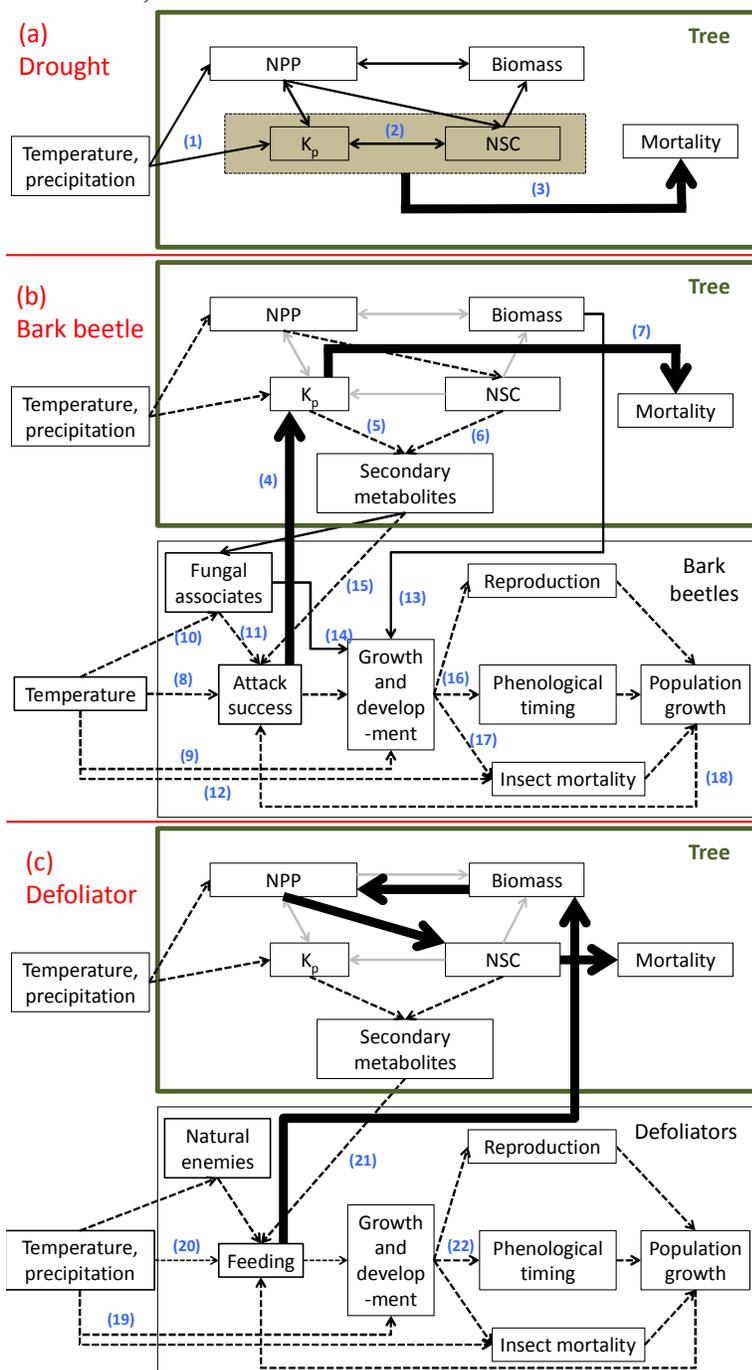
800

801 Figure 2: Example attribution of the relative roles of drought stress, insect attack, and their
 802 interactions in recent angiosperm (orange) and gymnosperm (blue) mortality events in western
 803 North America. References for episodes: *Juniperus ashei* mortality in Texas (Twidwell et al.
 804 2014); *Populus tremuloides* mortality (Worrall et al. 2008; Anderegg et al. 2012; 2013; Worrall
 805 et al. 2013); *Pinus edulis* mortality (Breshears et al. 2005; Gaylord et al. 2013; Meddens et al.
 806 2015); *Pinus contorta* mortality (Chapman et al. 2012); *Pinus albicaulis* mortality (Bentz et al.
 807 2013).



808
 809
 810
 811
 812
 813
 814
 815
 816
 817
 818
 819
 820

821 Figure 3: Conceptual framework of tree interactions with two insect guilds, illustrating tree
 822 mortality caused by climate and insects. Drought-induced tree mortality (a) occurs when climate
 823 variables influence net primary productivity (NPP) and plant hydraulic conductivity (K_p), which
 824 are interlinked with non-structural carbohydrate reserves (NSC) and biomass. In (b) and (c),
 825 insect feeding guilds of bark beetles and defoliators, respectively, are coupled with the tree
 826 model (green box) to lead to mortality. Thick black lines indicate pathways of tree mortality. In
 827 insect feeding guilds, dashed black lines indicate common links in both bark beetles and
 828 defoliators; solid black lines indicate differences between bark beetles and defoliators.



829