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

Authors: Jianbei Huang, Markus Kautz, Amy M. Trowbridge, Almuth Hammerbacher, Kenneth F. Raffa, Henry D. Adams, Devin W. Goodsman, Chonggang Xu, Arjan J.H. Meddens, Dineshkumar Kandasamy, Jonathan Gershenzon, Rupert Seidl and Henrik Hartmann

The following Supporting Information is available for this article:

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

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

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

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

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

Table S1 Common bark beetle species known to promote or cause significant mortality on conifers. Categorization of life history strategy is based on physiological condition of trees beetles commonly colonize, although this can vary with population phase (Raffa *et al.*, 1993).

| Common name | Scientific name | Common host | Known fungal symbionts | Life history strategy |
|---|---|---|---|---|
| Western Pine Beetle | *Dendroctonus brevicomis* | *Pinus coulteri, Pinus ponderosa* | *Entomocorticium* sp. B[1], *Ceratocystiopsis brevicomi*[2] | Primary |
| Southern Pine Beetle | *Dendroctonus frontalis* | *Pinus echinata, Pinus engelmanni, Pinus leiophylla, Pinus ponderosa, Pinus rigida, Pinus taeda, Pinus virginiana* | *Entomocorticium* sp. A, *Ceratocystiopsis ranaculosus*[3] | Primary |
| Jeffrey Pine Beetle | *Dendroctonus jeffreyi* | *Pinus jeffreyi* | *Grosmannia clavigera* | Secondary |
| Mountain pine Beetle | *Dendroctonus ponderosae* | *Pinus contorta, Pinus ponderosa, Pinus albicaulis* | *Grosmannia clavigera*[4], *Ophiostoma montium*[5] *Leptographium longiclavatum, Entomocorticium dendroctoni*[6] | Primary |
| Douglas-fir Beetle | *Dendroctonus pseudotsugae* | *Pseudotsuga menziesii* | *Ophiostoma pseudotsugae*[7], *Leptographium abietinum*[7] | Secondary |
| North American Spruce beetle | *Dendroconus rufipennis* | *Picea engelmannii, Picea glauca, Picea sitchensis* | *Leptographium abietinum*[8], *Endoconidiophora rufipenni*[8] | Primary |
| Eastern Larch Beetle | *Dendroctonus simplex* | *Larix larcina, Picea rubens* | | Secondary |
| Red turpentine beetle | *Dendroctonus valens* | North America: *Abies concolor*<br><br>Invasive to China: *Pinus tabuliformis, Pinus armandi* | *Leptographium terebrantis*[9], *Ophiostoma ips*[9], *Leptographium procerum*[9] *Leptographium sinoprocerum Ophiostoma minus*[10] | Secondary |
| Eastern Six-spined Engraver | *Ips calligraphus* | *Pinus echinata, Pinus elliotti, Pinus ponderosa, Pinus taeda, Pinus virginiana* | | Secondary |
| Eastern Five-spined Engraver | *Ips grandicollis* | *Pinus resinosa, Pinus radiate, Pinus taeda, Pinus banksiana*<br><br>Invasive to Australia: *Pinus radiata* | *Ophiostoma ips*[11] | Secondary |
| Piñon Ips | *Ips confusus* | *Pinus edulis, Pinus monophylla* | | Secondary |
| Arizona Five-spined Ips | *Ips lecontei* | *Pinus ponderosa* | | Secondary |
| Pine Engraver | *Ips pini* | *Pinus contorta, Pinus jeffreyi, Pinus lambertiana, Pinus ponderosa, Pinus resinosa* | *Ophiostoma ips*[12] | Secondary |
| European Spruce Bark Beetle | *Ips typographus* | *Picea abies* | *Endoconidiophora polonica*[13], *Grosmannia penicillata*[13], *Grosmannia europhioides*[13], *Ophiostoma bicolor*[13], *Ophiostoma ainoae*[13] | Primary |
| Fir Engraver | *Scolytus ventralis* | *Abies concolor, Abies grandis, Abies magnifica* | *Trichosporium symbioticum*[14] | Secondary |

[1]See citations within [1](Paine & Birch, 1983), [2](Tang-Wung Hsiau & Harrington, 1997), [3](Hofstetter & Moser, 2014), [4](Six & Paine, 1998) , [5](Six, 2003), [6](Six, 2012), [7](Paine *et al.*, 1997), [8](Solheim & Safranyik, 1997), [9](Six & Klepzig, 2004), [10](Wang *et al.*, 2012), [11](Smalley *et al.*, 1993), [12](Furniss *et al.*, 1995), [13](Kandasamy *et al.*, 2016), and [14](Livingston & Berryman, 1972).

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

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

Updated from Raffa *et al.* (2005), with Kopper *et al.* (2005), Adams *et al.* (2011), Hammerbacher *et al.* (2011), Reid and Purcell (2011), Boone *et al.* (2013), Hammerbacher *et al.* (2014), Mason *et al.* (2015), Reid *et al.* (2017), Chiu *et al.* (2017), Zhao *et al.* (2019), and Hammerbacher *et al.* (2019). The biological effects of secondary metabolites are shown as inhibitory (+) or untested (?).

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

| Year | Authors | Model name | Model type | Extent | Genus | Defense | Comment on defense mechanism |
|------|---------|-----------|-----------|--------|-------|---------|------------------------------|
| 2000 | Biesinger et al. | - | other | none | Dendroctonus | structure | |
| 2006 | Bone et al. | - | ABM | local | Dendroctonus | structure | |
| 2006 | Hughes et al. | - | ABM | local | Dendroctonus | structure | |
| 2007 | Seidl et al. | - | FLM | local | Ips | climate | Tree-based drought stress function |
| 2008 | Cairns et al. | Landis-BDA | FLM | local | Dendroctonus | structure | |
| 2008 | Nelson & Lewis | - | other | none | Dendroctonus | structure | NSC only implicitly considered |
| 2009 | Chubaty et al. | - | other | none | Dendroctonus | structure | |
| 2009 | Powell & Bentz | - | other | local | Dendroctonus | structure | |
| 2009 | Seidl et al. | PICUS-EFISCEN | FLM | regional | Ips | climate | Tree-based drought stress function |
| 2010 | Lewis et al. | - | other | none | n.s. | structure | |
| 2010 | Perez & Dragicevic | GIS-ABM | ABM | local | Dendroctonus | none | |
| 2011 | Edburg et al. | CLM4 | DGVM | local | Dendroctonus | none | |
| 2011 | Fahse & Heurich | SAMBIA | ABM | local | Ips | structure | |
| 2011 | Kausrud et al. | - | other | none | n.s. | structure | |
| 2011 | Pérez & Dragićević | ForestSimMPB | ABM | local | Dendroctonus | none | |
| 2012 | Jönsson et al. | LPJ-GUESS | DGVM | regional | Ips | climate | Tree-based drought stress threshold |
| 2013 | Temperli et al. | LandClim | FLM | local | Ips | climate | Tree-based drought stress function |
| 2014 | Bone & Altaweel | - | ABM | local | Dendroctonus | structure | |
| 2014 | Chen-Charpentier & Leite | - | other | none | n.s. | structure | |
| 2014 | Kautz et al. | IPS | ABM | local | Ips | structure | |
| 2015 | Temperli et al. | LandClim | FLM | local | Dendroctonus | climate | Tree-based drought stress function |
| 2015 | Duncan et al. | - | other | none | Dendroctonus | none | |
| 2015 | Régnière et al. | - | ABM | none | Dendroctonus | none | |
| 2016 | Křivan et al. | - | other | local | n.s. | none | |
| 2016 | Landry et al. | IBIS-MIM | DGVM | regional | Dendroctonus | none | |
| 2016 | Louis et al. | - | ABM | regional | Ips | structure | |
| 2017 | Loehman et al. | FireBGC | FLM | regional | Dendroctonus | none | Tree-based drought stress not applied to bark beetle susceptibility |
| 2017 | Seidl & Rammer | iLand | FLM | local | Ips | physiology | Tree-based NSC pool function |
| 2018 | Foster et al. | UVAFME | FLM | local | Dendroctonus | structure | Tree stress is growth-related, but not directly drought-related |
| 2018 | Honkaniemi et al. | BBDYN | ABM | local | Ips | structure | |
| 2018 | Kautz et al. | LPJ-GUESS | DGVM | continental | n.s. | none | |
| 2018 | Nelson et al. | - | ABM | local | Dendroctonus | structure | |
| 2018 | Scheller et al. | Landis-BDA | FLM | regional | n.s. | climate | Climatic drought index (PDSI) threshold |
| 2018 | Goodsman et al. | FATES-IMAP | DGVM | regional | Dendroctonus | structure | |

**Method S1**: Description of the Insect Mortality and Phenology module incorporated into the FATES-IMAP(Goodsman *et al.*, 2018)

FATES-IMAP is a dynamic global vegetation model which represents insect demography as a function of weather-related driving variables. Insect phenology and mortality are simulated using the integral projection approach for stochastic rate summation modeling. Currently, the IMAP extension of FATES only simulates tree mortality due to MPB attack. In the current FATES-IMAP model, MPB populations emerge in one-hectare habitat patches and attack trees locally within the patch. All patches are assumed to have endemic populations of beetles with demographics governed by weather fluctuations. At endemic levels, local MPB populations are assumed to persist in weakened trees either already dying of other causes or have highly compromised defences (Safranyik & Carroll, 2006). Once beetle populations exceed the endemic threshold, they attack vigorous host trees and their dynamics are henceforth governed by host availability in addition to weather.

In the FATES-IMAP model, the rate at which MPB attack host trees depends on the incipient-epidemic threshold, which is the minimum density of beetles on a per hectare basis that is required to overcome a single well-defended host tree (Carroll *et al.*, 2006). Researchers have estimated that, for MPB, the endemic threshold is approximately 40 beetles per hectare, whereas the incipient-epidemic threshold varies between 300 − 500 beetles per hectare (Carroll *et al.*, 2006). The FATES-IMAP model assumes that beetles are clustered within local one-hectare patches and it therefore uses the cumulative mass function of the negative binomial distribution instead of a step function to represent the probability of tree mortality as a function of local beetle density (Ives & May, 1985; Goodsman *et al.*, 2016; Goodsman *et al.*, 2017). The current version of the FATES-IMAP model does not vary the incipient-epidemic threshold as a function of carbohydrate availability or vigor. This means that the dynamic interplay between tree physiology, tree defence, and bark beetle infestations described in the previous sections is not captured in FATES-IMAP, but that the process representation in the model would allow for such dynamic interactions to be implemented.

**Method S2**: Host tree defense implementation in process-based bark beetle models

We employed an in-depth literature search targeting process-based bark beetle infestation models that were published in the years 2000 – 2018. Simulation studies without an explicit representation of the bark beetle infestation process, or follow-up studies applying the same bark beetle model to a different research question were not considered here.

Finally, screening resulted in 34 simulation studies from which we extracted the year and authors of publication, the model name and the following attributes (Table S3):

**Model type** – 4 types were differentiated: *´ABM´* (agent-based models), *´FLM´* (forest landscape models), *´DGVM´* (dynamic global vegetation models), and *´other´* (including models that can´t be assigned to one of the other types, e.g. ordinal- and partial differential equation models, non-spatial models)

**Extent** – areal extent of model application, 4 levels were differentiated: *´local´* ($1\text{-}10^2$ km²), *´regional´* ($10^3\text{-}10^5$ km²), *´continental´* ($>10^5$ km²), and *´none´* (including studies without an indication of extent of application)

**Genus** – bark beetle genus to which the model is applied, 3 groups were differentiated: *´Dendroctonus´* (D. ponderosae, D. rufipennis, D. frontalis), *´Ips´* (I. typographus), and *´n.s.´* (including models that simulate several genera, or that are not specifically parameterized for a single species or genus)

**Defense** – Defense mechanism against bark beetles applied in the model, 4 groups were differentiated: *´none´* (ignorance or rudimentary representation of tree defense, e.g. only determined by host species or tree size/age threshold), *´structure´* (determined by tree or stand parameters, e.g. tree size, age, DBH, basal area; pre-disturbances, e.g. fire, windthrow, and distance-to-previous infestations; or beetle population density), *´climate´* (considering climate sensitivity, e.g. tree-specific drought-stress indices), and *´physiology´* (considering tree physiological processes, i.e. NSC, that determine defense capacity). Following this hierarchical classification, the latter category typically comprises the former one.

The 34 reviewed models where applied to address a range of different research questions at varying spatial and temporal scales, thus they naturally differ in the level of process detail implemented. The growing attention to bark beetle models is reflected by the fact, that

almost half of the models have been published between 2014 and 2018. Overall, most models are parameterized for North American *Dendroctonus* species (55%), in comparison to mainly European *Ips* species (27%), or to non-species specific models (18%). Among model types ABMs (33%), FLMs (27%) and other types (27%) are most frequent; DGVMs (12%) instead scarcely simulate bark beetle disturbance yet. A quarter of models represent tree defense against bark beetles only rudimentary or even ignore it, while in the remaining models (72%) structural parameters play a major role, with climate- or tree physiology-based parameters (18% and 3%, respectively) being far less represented.

## References

**Adams AS, Boone CK, Bohlmann J, Raffa KF. 2011.** Responses of bark beetle-associated bacteria to host monoterpenes and their relationship to insect life histories. *Journal of Chemical Ecology* **37**: 808-817.

**Biesinger Z, Powell J, Bentz B, Logan J. 2000.** Direct and indirect parametrization of a localized model for the mountain pine beetle — lodgepole pine system. *Ecological Modelling* **129**: 273-296.

**Bone C, Dragicevic S, Roberts A. 2006.** A fuzzy-constrained cellular automata model of forest insect infestations. *Ecological Modelling* **192**: 107-125.

**Bone C, Altaweel M. 2014.** Modeling micro-scale ecological processes and emergent patterns of mountain pine beetle epidemics. *Ecological Modelling* **289**: 45-58.

**Boone CK, Keefover-Ring K, Mapes AC, Adams AS, Bohlmann J, Raffa KF. 2013.** Bacteria associated with a tree-killing insect reduce concentrations of plant defense compounds. *Journal of Chemical Ecology* **39**: 1003-1006.

**Cairns DM, Lafon CW, Waldron JD, Tchakerian M, Coulson RN, Klepzig KD, Birt AG, Xi W. 2008.** Simulating the reciprocal interaction of forest landscape structure and southern pine beetle herbivory using LANDIS. *Landscape Ecology* **23**: 403-415.

**Carroll LA, Aukema B, Raffa K, Linton AD, Smith G, Lindgren BS. 2006.** Mountain pine beetle outbreak development: the endemic - incipient epidemic transition. Canadian Forest Service, Mountain Pine Beetle Initiative Project.

**Chen-Charpentier B, Leite MCA. 2014.** A model for coupling fire and insect outbreak in forests. *Ecological Modelling* **286**: 26-36.

**Chiu CC, Keeling CI, Bohlmann J. 2017.** Toxicity of pine monoterpenes to mountain pine beetle. *Scientific Reports* **7**: 8858.

**Chubaty AM, Roitberg BD, Li C. 2009.** A dynamic host selection model for mountain pine beetle, Dendroctonus ponderosae Hopkins. *Ecological Modelling* **220**: 1241-1250.

**Duncan JP, Powell JA, Gordillo LF, Eason J. 2015.** A model for mountain pine beetle outbreaks in an age-structured forest: predicting severity and outbreak-recovery cycle period. *Bulletin of Mathematical Biology* **77**: 1256-1284.

**Edburg SL, Hicke JA, Lawrence DM, Thornton PE. 2011.** Simulating coupled carbon and nitrogen dynamics following mountain pine beetle outbreaks in the western United States. *Journal of Geophysical Research-Biogeosciences* **116**: G04033.

**Fahse L, Heurich M. 2011.** Simulation and analysis of outbreaks of bark beetle infestations and their management at the stand level. *Ecological Modelling* **222**: 1833-1846.

**Foster AC, Shuman JK, Shugart HH, Negron J. 2018.** Modeling the interactive effects of spruce beetle infestation and climate on subalpine vegetation. *Ecosphere* **9**: e02437.

**Furniss MM, Harvey EA, Solheim H. 1995.** Transmission of *Ophiostoma ips* (Ophiostomatales: Ophiostomataceae) by *Ips pini* (Coleoptera: Scolytidae) to Ponderosa Pine in Idaho. *Annals of the Entomological Society of America* **88**: 653-660.

**Goodsman DW, Koch D, Whitehouse C, Evenden ML, Cooke BJ, Lewis MA. 2016.** Aggregation and a strong Allee effect in a cooperative outbreak insect. *Ecological Applications* **26**: 2623-2636.

**Goodsman DW, Cooke BJ, Lewis MA. 2017.** Positive and negative density-dependence and boom-bust dynamics in enemy-victim populations: a mountain pine beetle case study. *Theoretical Ecology* **10**: 255-267.

**Goodsman DW, Aukema BH, McDowell NG, Middleton RS, Xu C. 2018.** Incorporating variability in simulations of seasonally forced phenology using integral projection models. *Ecology and Evolution* **8**: 162-175.

**Hammerbacher A, Ralph SG, Bohlmann J, Fenning TM, Gershenzon J, Schmidt A. 2011.** Biosynthesis of the major tetrahydroxystilbenes in spruce, astringin and isorhapontin, proceeds via resveratrol and is enhanced by fungal infection. *Plant Physiology* **157**: 876-890.

**Hammerbacher A, Paetz C, Wright LP, Fischer TC, Bohlmann J, Davis AJ, Fenning TM, Gershenzon J, Schmidt A. 2014.** Flavan-3-ols in Norway spruce: biosynthesis, accumulation, and function in response to attack by the bark beetle-associated fungus *Ceratocystis polonica*. *Plant Physiology* **164**: 2107-2122.

**Hammerbacher A, Kandasamy D, Ullah C, Schmidt A, Wright LP, Gershenzon J. 2019.** Flavanone-3-Hydroxylase plays an important role in the biosynthesis of spruce phenolic defenses against bark beetles and their fungal associates. *Frontiers in Plant Science* **10**: 208.

**Hofstetter RW, Moser JC. 2014.** The role of mites in insect-fungus associations. *Annual Review of Entomology* **59**: 537-557.

**Honkaniemi J, Ojansuu R, Kasanen R, Heliövaara K. 2018.** Interaction of disturbance agents on Norway spruce: A mechanistic model of bark beetle dynamics integrated in simulation framework WINDROT. *Ecological Modelling* **388**: 45-60.

**Hughes J, Fall A, L S, k L 2006.** Modeling the effect of landscape pattern on mountain pine bettles. Victoria, British Columbia: Natural Resources Canada, Canadian Forest Service, Information Report BC-X-407, 464 pp.

**Ives AR, May RM. 1985.** Competition within and between species in a patchy environment: Relations between microscopic and macroscopic models. *Journal of Theoretical Biology* **115**: 65-92.

**Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B. 2012.** Guess the impact of *Ips typographus*-An ecosystem modelling approach for simulating spruce bark beetle outbreaks. *Agricultural and Forest Meteorology* **166**: 188-200.

**Kandasamy D, Gershenzon J, Hammerbacher A. 2016.** Volatile organic compounds emitted by fungal associates of conifer bark beetles and their potential in bark beetle control. *Journal of Chemical Ecology* **42**: 952-969.

**Kausrud KL, Gregoire JC, Skarpaas O, Erbilgin N, Gilbert M, Okland B, Stenseth NC. 2011.** Trees wanted—dead or alive! Host selection and population dynamics in tree-killing bark beetles. *Plos One* **6**: e18274.

**Kautz M, Schopf R, Imron MA. 2014.** Individual traits as drivers of spatial dispersal and infestation patterns in a host–bark beetle system. *Ecological Modelling* **273**: 264-276.

**Kautz M, Anthoni P, Meddens AJH, Pugh TAM, Arneth A. 2018.** Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States. *Global Change Biology* **24**: 2079-2092.

**Kopper BJ, Illman BL, Kersten PJ, Klepzig KD, Raffa KF. 2005.** Effects of diterpene acids on components of a conifer bark beetle–fungal interaction: tolerance by *Ips pini* and sensitivity by its associate *Ophiostoma ips*. *Environmental Entomology* **34**: 486-493.

**Krivan V, Lewis M, Bentz BJ, Bewick S, Lenhart SM, Liebhold A. 2016.** A dynamical model for bark beetle outbreaks. *Journal of Theoretical Biology* **407**: 25-37.

**Landry JS, Price DT, Ramankutty N, Parrott L, Matthews HD. 2016.** Implementation of a Marauding Insect Module (MIM, version 1.0) in the Integrated BIosphere Simulator (IBIS, version 2.6b4) dynamic vegetation-land surface model. *Geoscientific Model Development* **9**: 1243-1261.

**Lewis MA, Nelson W, Xu CL. 2010.** A structured threshold model for mountain pine beetle outbreak. *Bulletin of Mathematical Biology* **72**: 565-589.

**Livingston RL, Berryman AA. 1972.** Fungus transport structures in the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). *Canadian Entomologist* **104**: 1793-1800.

**Loehman RA, Keane RE, Holsinger LM, Wu ZW. 2017.** Interactions of landscape disturbances and climate change dictate ecological pattern and process: spatial modeling of wildfire, insect, and disease dynamics under future climates. *Landscape Ecology* **32**: 1447-1459.

**Louis M, Toffin E, Gregoire JC, Deneubourg JL. 2016.** Modelling collective foraging in endemic bark beetle populations. *Ecological Modelling* **337**: 188-199.

**Mason CJ, Klepzig KD, Kopper BJ, Kersten P, Illman BL, Raffa KF. 2015.** Contrasting patterns of diterpene acid induction by red pine and white spruce to simulated bark beetle attack, and interspecific differences in sensitivity among fungal associates. *Journal of Chemical Ecology* **41**: 524-532.

**Nelson MF, Murphy JT, Bone C, Altaweel M. 2018.** Cyclic epidemics, population crashes, and irregular eruptions in simulated populations of the mountain pine beetle, Dendroctonus ponderosae. *Ecological Complexity* **36**: 218-229.

**Nelson WA, Lewis MA. 2008.** Connecting host physiology to host resistance in the conifer-bark beetle system. *Theoretical Ecology* **1**: 163-177.

**Paine T, Birch CM. 1983.** Acquisition and maintenance of mycangial fungi by *Dendroctonus brevicomis* LeConte (Coleoptera: Scolytidae). **12**: 1384-1386.

**Paine TD, Raffa KF, Harrington TC. 1997.** Interactions among scolytid bark beetles, their associated fung, and live host conifers. *Annual Review of Entomology* **42**: 179-206.

**Perez L, Dragicevic S. 2010.** Modeling mountain pine beetle infestation with an agent-based approach at two spatial scales. *Environmental Modelling & Software* **25**: 223-236.

**Pérez L, Dragićević S. 2011.** ForestSimMPB: A swarming intelligence and agent-based modeling approach for mountain pine beetle outbreaks. *Ecological Informatics* **6**: 62-72.

**Powell JA, Bentz BJ. 2009.** Connecting phenological predictions with population growth rates for mountain pine beetle, an outbreak insect. *Landscape Ecology* **24**: 657-672.

**Raffa KF, Phillips TW, Salom SM. 1993.** Strategies and mechanisms of host colonization by bark beetles. *Beetle-pathogen interactions in conifer forests*: 103-128.

**Raffa KF, Aukema B, Erbilgin N, Klepzig K, Wallin K 2005.** Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. In: Romeo JT ed. *Recent Advances in Phytochemistry*. Toronto, Canada: Elsevier, 79-118.

**Régnière J, Bentz BJ, Powell JA, St-Amant R 2015.** Individual-based modeling: mountain pine beetle seasonal biology in response to climate. In: Perera AH, Sturtevant BR, Buse LJ eds. *Simulation modeling of forest landscape disturbances*. Cham: Springer International Publishing, 135-164.

**Reid ML, Purcell JRC. 2011.** Condition-dependent tolerance of monoterpenes in an insect herbivore. *Arthropod-Plant Interactions* **5**: 331-337.

**Reid ML, Sekhon JK, LaFramboise LM. 2017.** Toxicity of monoterpene structure, diversity and concentration to mountain pine beetles, *Dendroctonus ponderosae*: beetle traits matter more. *Journal of Chemical Ecology* **43**: 351-361.

**Safranyik L, Carroll AL 2006.** The biology and epidemiology of the mountain pine beetle in lodgepole pine forests. In: Safranyik L, Wilson B eds. *The mountain pine beetle: a synthesis of its biology, management and impacts on lodgepole pine.* Victoria, British Columbia: Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, 3-66.

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

**Seidl R, Baier P, Rammer W, Schopf A, Lexer MJ. 2007.** Modelling tree mortality by bark beetle infestation in Norway spruce forests. *Ecological Modelling* **206**: 383-399.

**Seidl R, Schelhaas MJ, Lindner M, Lexer MJ. 2009.** Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. *Regional Environmental Change* **9**: 101-119.

**Seidl R, Rammer W. 2017.** Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Landscape Ecology* **32**: 1485-1498.

**Six D 2003.** Bark Beetle-fungus Symbioses. In: Bourtzis K, Miller T eds. *Insect symbiosis*. Boca Raton, FL: CRC Press, 97-114.

**Six D, Klepzig K. 2004.** Dendroctonus bark beetles as model systems for studies on symbiosis. *Symbiosis* **37**: 207-232.

**Six DL, Paine TD. 1998.** Effects of Mycangial Fungi and Host Tree Species on Progeny Survival and Emergence of Dendroctonus ponderosae (Coleoptera: Scolytidae). *Environmental Entomology* **27**: 1393-1401.

**Six DL. 2012.** Ecological and evolutionary determinants of bark beetle-fungus symbioses. *Insects* **3**: 339-366.

**Smalley EB, Raffa KF, Proctor RH, Klepzig KD 1993.** Tree responses to infection by species of *Ophiostoma* and *Ceratocystis*. In: Wingfield MJ, Seifert KA, Webber JF eds. *Taxonomy, Ecology, and Pathogenicity*. Minnesota: APS Press, St. Paul, 207-217.

**Solheim H, Safranyik L. 1997.** Pathogenicity of the spruce beetle associated blue-stain fungi, *Ceratocystis rufipenni* and *Leptographium abietinum* to Sitka spruce. *Canadian Journal of Forest Research* **27**: 1336-1341.

**Tang-Wung Hsiau P, Harrington T. 1997.** *Ceratocystiopsis brevicomi* sp. nov., a mycangial fungus from *Dendroctonus brevicomis* (Coleoptera: Scolytidae). *Mycologia* **89**: 661.

**Temperli C, Bugmann H, Elkin C. 2013.** Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. *Ecological Monographs* **83**: 383-402.

**Temperli C, Veblen TT, Hart SJ, Kulakowski D, Tepley AJ. 2015.** Interactions among spruce beetle disturbance, climate change and forest dynamics captured by a forest landscape model. *Ecosphere* **6**: art231.

**Wang B, Lu M, Cheng C, Salcedo C, Sun J. 2012.** Saccharide-mediated antagonistic effects of bark beetle fungal associates on larvae. *Biology Letters* **9**: 1-4.

**Zhao T, Kandasamy D, Krokene P, Chen J, Gershenzon J, Hammerbacher A. 2019.** Fungal associates of the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer phenolics and influence bark beetle tunneling behavior. *Fungal Ecology* **38**: 71-79.