

## ***New Phytologist* Supporting Information**

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

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

<sup>1</sup>See citations within <sup>1</sup>(Paine & Birch, 1983), <sup>2</sup>(Tang-Wung Hsiau & Harrington, 1997), <sup>3</sup>(Hofstetter & Moser, 2014), <sup>4</sup>(Six & Paine, 1998) , <sup>5</sup>(Six, 2003), <sup>6</sup>(Six, 2012), <sup>7</sup>(Paine *et al.*, 1997), <sup>8</sup>(Solheim & Safranyik, 1997), <sup>9</sup>(Six & Klepzig, 2004), <sup>10</sup>(Wang *et al.*, 2012), <sup>11</sup>(Smalley *et al.*, 1993), <sup>12</sup>(Furniss *et al.*, 1995), <sup>13</sup>(Kandasamy *et al.*, 2016), and <sup>14</sup>(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 & Dragičević	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*’ (1-10<sup>2</sup> km<sup>2</sup>), ‘*regional*’ (10<sup>3</sup>-10<sup>5</sup> km<sup>2</sup>), ‘*continental*’ (>10<sup>5</sup> km<sup>2</sup>), 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 were 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.

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