

# Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States

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1                   **Simulating the recent impacts of multiple biotic disturbances**  
2                   **on forest carbon cycling across the United States**

3  
4  
5 **Running head:**       Biotic disturbance impacts across US forests

6  
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26 **Abstract**

27 Biotic disturbances (BDs, e.g., insects, pathogens and wildlife herbivory) substantially affect  
28 boreal and temperate forest ecosystems globally. However, accurate impact assessments  
29 comprising larger spatial scales are lacking to date, although these are critically needed given  
30 the expected disturbance intensification under a warming climate. Hence, our quantitative  
31 knowledge on current and future BD impacts, e.g., on forest carbon (C) cycling, is strongly  
32 limited. We extended a Dynamic Global Vegetation Model to simulate ecosystem response to  
33 prescribed tree mortality and defoliation due to multiple biotic agents across United States  
34 forests during the period 1997-2015, and quantified the BD-induced vegetation C loss, i.e., C  
35 fluxes from live vegetation to dead organic matter pools. Annual disturbance fractions  
36 separated by BD type (tree mortality and defoliation) and agent (bark beetles, defoliator  
37 insects, other insects, pathogens, and other biotic agents) were calculated at 0.5° resolution  
38 from aerial-surveyed data and applied within the model. Simulated BD-induced C fluxes  
39 totaled 251.6 Mt C (annual mean: 13.2 Mt C yr<sup>-1</sup>, SD ±7.3 Mt C yr<sup>-1</sup> between years) across the  
40 study domain, to which tree mortality contributed 95% and defoliation 5%. Among BD  
41 agents, bark beetles caused most C fluxes (61%), and total insect-induced C fluxes were about  
42 five times larger compared to non-insect agents, e.g., pathogens and wildlife. Our findings  
43 further demonstrate that BD-induced C cycle impacts (i) displayed high spatio-temporal  
44 variability, (ii) were dominated by different agents across BD types and regions, and (iii) were  
45 comparable in magnitude to fire-induced impacts. This study provides the first ecosystem  
46 model-based assessment of BD-induced impacts on forest C cycling at the continental scale  
47 and going beyond single agent-host systems, thus allowing for comparisons across regions,  
48 BD types and agents. Ultimately, a perspective on the potential and limitations of a more  
49 process-based incorporation of multiple BDs in ecosystem models is offered.

## 50 INTRODUCTION

51 Natural disturbances, such as fire, windthrow, insect and pathogen outbreaks, are key drivers  
52 of vegetation dynamics and significantly affect the structure and functioning of forest  
53 ecosystems (Turner, 2010; Battisti *et al.*, 2016). Forest disturbances are manifested by a  
54 complete (tree mortality) or partial loss of living tree biomass and/or tree functionality (e.g.,  
55 defoliation, crown breakage), which may occur from local to landscape scales. While  
56 disturbances are thus often associated with a temporal decline in ecosystem service provision,  
57 such as carbon (C) sequestration, they also enhance renewal and structural diversity, and  
58 thereby contribute to forest stability (Boyd *et al.*, 2013; Thom & Seidl, 2016). However, the  
59 intensification of natural disturbance regimes caused by global warming (Dale *et al.*, 2001;  
60 Seidl *et al.*, 2017), may reduce ecosystem resilience and ultimately lead to sustained  
61 ecosystem transitions (Johnstone *et al.*, 2016).

62 Biotic disturbances (BDs), i.e., damage caused by insects, pathogens, or other biotic agents,  
63 have affected global forests in recent decades, in particular northern boreal and temperate  
64 forests (van Lierop *et al.*, 2015; Kautz *et al.*, 2017). Extensive BD-induced tree mortality and  
65 defoliation has been reported for Canada and the United States due to bark beetles, e.g.,  
66 mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*D. rufipennis*), and southern  
67 pine beetle (*D. frontalis*); defoliating insects, e.g., western and eastern spruce budworm  
68 (*Choristoneura occidentalis*, *C. fumiferana*), forest tent caterpillar (*Malacosoma disstria*), and  
69 gypsy moth (*Lymantria dispar*); sap-feeding insects, e.g., hemlock and balsam woolly  
70 adelgid, (*Adelges tsugae*, *A. piceae*); as well as due to pathogens, e.g., *Phytophthora ramorum*  
71 causing sudden oak death, and *Ophiostoma* spp. causing Dutch elm disease (Canadian Forest  
72 Service, 2017; USDA Forest Service, 2017). Such outbreaks have the potential to impact  
73 multiple biochemical and biophysical processes for weeks to decades.

74 Forest productivity, i.e., gross and net primary productivity (GPP, NPP) and net ecosystem  
75 productivity (NEP), is generally reduced by BDs. Magnitude and duration of the reduction,  
76 however, differ substantially between tree mortality and defoliation (Hicke *et al.*, 2012;  
77 Flower & Gonzales-Meler, 2015; Cooper *et al.*, 2017). Defoliation, not resulting in  
78 subsequent tree mortality, only temporarily reduces photosynthesis, thereby decreasing  
79 growth performance, and thus plant net C uptake. Depending on the severity of defoliation,  
80 this leads to a reduced C sink capacity of the affected forest, or might even create a short-term  
81 C source (e.g., Clark *et al.*, 2010). Typically, trees are capable of recovering foliage and  
82 functionality completely once agent pressure is released. In contrast to non-lethal defoliation,  
83 tree mortality results in larger and more sustained negative effects on productivity. The  
84 combination of increased heterotrophic respiration and decreased NPP results in a negative  
85 NEP immediately following tree mortality, which then typically recovers to levels seen pre-  
86 disturbance (Edburg *et al.*, 2012; Anderegg *et al.*, 2016). As a consequence, affected forests  
87 might function as a C source over few years (Brown *et al.*, 2012) up to decades (Kurz *et al.*,  
88 2008), with magnitude and duration depending on initial tree mortality fraction and the speed  
89 of decomposition and regrowth (Anderegg *et al.*, 2016). In addition to C cycle impacts, BDs  
90 have also been shown to alter forest dynamics and composition (Temperli *et al.*, 2015;  
91 Crowley *et al.*, 2016; Costilow *et al.*, 2017), energy, water, and nitrogen (N) fluxes (Bright *et*  
92 *al.*, 2013; Chen *et al.*, 2015; Anderegg *et al.*, 2016), as well as the emission of biogenic  
93 volatile organic compounds to the atmosphere (Berg *et al.*, 2013; Duhl *et al.*, 2013).

94 Despite the undoubted relevance of BDs for shaping global forest ecosystems and influencing  
95 vegetation-climate feedbacks, impact assessments remain scarce at the larger spatial scale,  
96 i.e., beyond the local-to-regional context, and mainly focused on single agent-host systems.  
97 Process-based ecosystem models such as Dynamic Global Vegetation Models (DGVMs) are  
98 prime tools for investigating feedbacks between climate, vegetation, and disturbances over

99 time and for quantifying terrestrial C cycle dynamics (Fisher *et al.*, 2014); however,  
100 incorporating BDs into these models is challenging due to the diversity and complexity of  
101 processes involved. Though the need for their incorporation has been repeatedly claimed for  
102 almost two decades now (Malmström & Raffa, 2000; Running, 2008; Arneth & Niinemets,  
103 2010; Quillet *et al.*, 2010), BDs are typically very generically represented in current-  
104 generation DGVMs, e.g., as part of a spatio-temporally constant ‘background’ disturbance  
105 mortality rate integrating over several mortality processes that are not explicitly implemented  
106 elsewhere in the model (Kautz *et al.*, 2017). In cases where DGVMs have been extended  
107 towards a more explicit simulation of BD dynamics and impacts (e.g., Edburg *et al.*, 2011;  
108 Jönsson *et al.*, 2012; Medvigy *et al.*, 2012; Landry *et al.*, 2016), approaches (i) have focused  
109 on a single disturbance agent-host system only (one agent species affecting one host plant  
110 functional type, PFT), (ii) were restricted to insects (excluding pathogens and other BDs) and  
111 (iii) were limited in their spatial coverage (landscape to regional scales). Forest Landscape  
112 Models (FLMs), though typically operating at much finer spatio-temporal scales and process  
113 resolution than DGVMs, have also been applied to simulate ecosystem impacts at the  
114 landscape scale due to insects, pathogens and/or wildlife herbivory (e.g., Temperli *et al.*,  
115 2015; Loehman *et al.*, 2017; Seidl & Rammer, 2017; De Jager *et al.*, 2017). For details on  
116 how BDs were considered in previous modelling approaches we refer the reader to S1 in the  
117 Supplementary Information where an overview is provided. To date, neither DGVMs nor  
118 FLMs has been applied at continental scales or larger, and considered multiple agent-host  
119 systems, thus limiting comparisons among different BD agents and regions.

120 This study aims to overcome these limitations by presenting a modelling approach that  
121 incorporates prescribed, spatio-temporally explicit disturbance fractions into a DGVM. By  
122 extending the model framework and applying comprehensive empirical disturbance data BD-  
123 induced impacts on forest C dynamics are simulated. In particular, we focus on quantifying

124 the vegetation C loss, which is the amount of C that is transferred from living tree biomass to  
125 dead organic matter pools, as a consequence of BD-induced tree mortality and defoliation,  
126 and on assessing the relative importance of the different biotic agents on C cycling across US  
127 forests from 1997 to 2015.

128

## 129 **MATERIAL & METHODS**

### 130 *Biotic disturbance data*

131 The US Insect and Disease Survey database (IDS, USDA Forest Service, 2017), as used in  
132 this study, contains aerial-surveyed, annual and spatially explicit information of BD-induced  
133 forest disturbance across the 48 lower states and Alaska over the years 1997-2015. This data  
134 set is globally unique in respect to its extensive coverage and long-term consistency,  
135 combined with a high spatial, temporal, and attributive resolution (Kautz *et al.*, 2017). It  
136 consists of a freely accessible ArcGIS geodatabase containing approximately 3 million  
137 attributed BD polygons. Non-BD polygons in the IDS, e.g., abiotic disturbances, were  
138 excluded for this study. Disturbance polygons have been manually sketch-mapped during  
139 annual survey flights covering most of the US forests (Johnson & Wittwer, 2008). Each  
140 polygon is accompanied with several attributes, e.g., the BD type (tree mortality, defoliation,  
141 discoloration, topkill, among others), the causal BD agent and the affected host tree (both  
142 mainly given at species level). Further attributes characterizing damage severity and pattern  
143 would also provide valuable information, yet they have been inconsistently recorded over the  
144 spatio-temporal domain of the study and have thus not been included in the analysis herein.  
145 The rapid, subjective process of in-flight polygon delineation and attribution limits detection  
146 accuracy, and thus data may involve a certain level of generalization and inherent uncertainty  
147 (e.g., discussed in Meddens *et al.*, 2012; Kautz *et al.*, 2017). For instance, areas assigned as

148 affected encompass healthy trees amongst damaged ones, which must be accounted for when  
149 reporting actual disturbed area (Meddens *et al.*, 2012). It should be also noted, that different  
150 polygons may spatially overlap within-year and between years. Both limitations were  
151 considered in the data processing described below. For details on standards of data acquisition  
152 and provision we refer the reader to the IDS documentation with updated Appendices E and F  
153 (USDA Forest Service, 2005).

154 Several processing steps were applied to the raw IDS data (using ArcGIS 10.2), to produce a  
155 nationwide gridded map of disturbance fractions which were then used as model input:  
156 initially, we merged the different regions for which the data was provided separately for each  
157 single year of the 19-year period, and selected the data regarding two attributes: the BD type  
158 and the causal BD agent. While separating the two major BD types, tree mortality and  
159 defoliation, we did not consider other types with less consequence for the C cycle, e.g.,  
160 discoloration and topkill. BD agents were classified into five groups, mainly according to  
161 feeding guilds or disturbance mechanisms, and based on the category as listed in the  
162 Appendix E in USDA Forest Service (2005): (1) bark beetles, (2) defoliator insects, (3) other  
163 insects, (4) pathogens, and (5) other biotic agents. The latter group comprises all non-insect  
164 and non-pathogen agents, but also includes BDs which could not be clearly assigned to  
165 another agent group, i.e., BDs caused by multiple biotic agents (e.g., insects *and* pathogens),  
166 or by interactions with abiotic factors (e.g., drought). All five agent groups may cause tree  
167 mortality and/or defoliation. An overview of the agent groups is provided in Table 1.

168 Forest cover information for the study domain was obtained from the GLC2000 data set – a  
169 satellite-based global land cover classification for the year 2000 (Bartolomé & Belward,  
170 2005), with vegetation classes 1 to 10 considered as forest in our analysis. We then created a  
171  $0.5^\circ \times 0.5^\circ$  grid layer that was consistent with the model resolution, and intersected this grid  
172 with the disturbance data and the forest cover data. To account for within-year overlapping of



173 polygons of similar BD types or agents we merged such polygons in a grid cell. Finally, we  
174 calculated the disturbance fraction  $D_f$  (% , =disturbed area / forest area  $\times$  100) for each grid  
175 cell and year separately for the selected BD types and agent groups. As an example, a grid cell  
176 might have been disturbed in a certain year by more than one type and/or agent, e.g., with  $D_f$   
177  $_{[\text{bark beetles}]}=3\%$ ,  $D_f_{[\text{defoliators}]}=1\%$  and  $D_f_{[\text{pathogens}]}=1.5\%$  for tree mortality, and  $D_f_{[\text{defoliators}]}$   
178  $=2.2\%$ ,  $D_f_{[\text{other insects}]}=1.7\%$  and  $D_f_{[\text{pathogens}]}=1.2\%$  for defoliation, giving a total disturbed  
179 fraction of 10.6%, of which 5.5% was mortality and 5.1% was defoliation.

180 To account for overestimation of BD extent due to healthy trees encompassed in delineated  
181 disturbance polygons, we applied a correction factor ( $CF$ ) on the calculated BD fractions  $D_f$  to  
182 get a deflated, more realistic fraction  $D'_f$  to be used for simulations:  $D'_f=CF \times D_f$ . In our study  
183 we generically applied  $CF=0.1$ , a factor that is in accordance with previous studies (Kurz &  
184 Apps, 1999; Meddens *et al.*, 2012), and explored effects of modified  $CF$  in the sensitivity  
185 analysis.

186 **Table 1.** Agent groups with associated categories and example species according to the  
 187 applied survey classification; for the complete list of IDS categories and species see Appendix  
 188 E in USDA Forest Service (2005)

| Agent group         | IDS category                                                                                                                               | Example species <sup>1</sup>                                                                                       |
|---------------------|--------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------|
| Bark beetles        | Bark beetles, boring insects                                                                                                               | <i>Dendroctonus</i> , <i>Ips</i> , <i>Scolytus</i> ,<br><i>Agrilus</i> , <i>Anoplophora</i> ,<br><i>Rhyacionia</i> |
| Defoliators         | Defoliators                                                                                                                                | <i>Choristoneura</i> , <i>Lymantria</i> ,<br><i>Malacosoma</i> ,<br><i>Neodiprion</i> , <i>Operophtera</i>         |
| Other insects       | General, sucking, chewing, gallmaker,<br>predator, root, seed/cone/flower/fruit,<br>terminal/shoot/twig insects                            | <i>Adelges</i> , <i>Conophthorus</i> ,<br><i>Megastigmus</i> , <i>Tomicus</i> ,<br><i>Matsucoccus</i>              |
| Pathogens           | General, root/butt, foliage diseases,<br>stem decays/cankers, stem/broom rusts                                                             | <i>Armillaria</i> , <i>Botryodiplodia</i> ,<br><i>Nectria</i> , <i>Phellinus</i> ,<br><i>Phytophthora</i>          |
| Other biotic agents | Parasitic/epiphytic plants, decline<br>complexes/dieback/wilts <sup>2</sup> , wild animals,<br>multi-damage (insect/disease <sup>2</sup> ) | Mistletoe, bears, hemlock<br>decline, pinyon pine<br>mortality                                                     |

189 <sup>1</sup> Insect and pathogen species were listed by genus names most representative for the agent  
 190 group, but note that in exceptional cases species from one genus may belong to multiple agent  
 191 groups.

192 <sup>2</sup> This category partially involves insects and/or pathogens.

193

194 ***LPJ-GUESS model***

195 In this study we used a DGVM with an advanced representation of forest stand dynamics, the  
 196 Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS). The model simulates  
 197 vegetation dynamics, including demography, in response to varying environmental conditions

198 and feedbacks between vegetation and soil (Smith *et al.*, 2001, 2014). Forest vegetation is  
199 represented by different PFTs (9 tree and two grass PFTs in this study), which are further  
200 distinguished in age cohorts. Stochastic processes associated with representation of growth  
201 and mortality are accounted for by the simulation (and averaging) of several replicate patches  
202 (20 in this study) for each of the  $0.5^\circ \times 0.5^\circ$  grid cells. Fire disturbances are modelled  
203 prognostically based on temperature, fuel load and moisture (Thonicke *et al.*, 2001), while  
204 stand-clearing `background` disturbances affect each patch randomly by a generic fraction of  
205  $0.01 \text{ yr}^{-1}$  (Smith *et al.*, 2014); these baseline settings for non-biotic disturbances were not  
206 changed for this study.

207 Following a spin-up period of 500 years, the model was forced by gridded input considering  
208 variant land use patterns (LUH2; Hurtt *et al.*, 2016, as applied in Bayer *et al.*, 2017), and  
209 CRUNCEP climate, CO<sub>2</sub> concentration, and N deposition that were identical to simulations  
210 used in the global carbon project (Le Quéré *et al.*, 2016). Specifically for this study, a gridded  
211 annual BD fraction map ( $0.5^\circ \times 0.5^\circ$ , described above) was applied for the period 1997-2015  
212 in addition to other forcing, in order to prescribe fractions of tree mortality and defoliation  
213 caused by biotic agents.

214

### 215 ***Disturbance extension***

216 We developed an extension to the current model framework, which improves the  
217 representation of stochastic disturbance events, e.g., due to biotic agents as presented in this  
218 study, or due to abiotic stressors like fire, storm, frost and drought. The extension allows for  
219 applying annually-prescribed disturbance fractions regarding two principal disturbance types,  
220 tree mortality and defoliation, for any given time period or region across the globe and

221 irrespective of the causal agent or stressor. Though the extension is principally applicable also  
222 to abiotic disturbances in this study it was only applied for BDs.

223 BD-induced tree mortality and defoliation events are implemented in slightly different ways  
224 in the model. Tree mortality is simulated as loss of a fraction of tree biomass, as prescribed in  
225 our BD dataset described above. Mortality occurs annually on day 365 of each year, as  
226 applied for other simulated tree mortality processes in the model, for instance, competition or  
227 bioclimatic constraints. Defoliation leads to a partial loss of leaf biomass only and affects tree  
228 age cohorts according to the prescribed defoliation fraction which is simulated to occur at a  
229 specific day of defoliation during the vegetation period. Here we used day of defoliation 180,  
230 i.e., end of June, a date that reflects the typical attack period (e.g., Schäfer *et al.*, 2010;  
231 Medvigy *et al.*, 2012). However, for C flux assessments in the model the day of defoliation  
232 has minimal influence, since C pool transfers are implemented at annual scale occurring at the  
233 end of each year. We further made the simplifying assumption that defoliated trees do not  
234 reflush their foliage within the same vegetation period, yet they may fully recover foliage in  
235 the following year.

236 Since disturbances are typically not equally distributed over different age cohorts within a  
237 grid cell, a minimum tree age threshold ( $TA$ ) is used to select for potential host trees. Hence,  
238 BD-induced mortality and defoliation only affects such tree cohorts that are  $\geq TA$  reflecting  
239 that aerial survey-based BD fractions mainly depict damage on canopies of larger over-story  
240 trees, and that young immature trees are typically less susceptible to BD (Hansen & Michaels  
241 Goheen, 2000; Hicke & Jenkins, 2008; Dymond *et al.*, 2010). Here we assumed  $TA=20$  years  
242 as most plausible threshold regarding both criteria, a value which is also in general  
243 accordance to field observations (e.g., Hawkins *et al.*, 2012) and previous modelling  
244 approaches (Table S1). Consequently, younger trees with  $TA < 20$  remained undisturbed by  
245 biotic agents in our simulations. For simplicity,  $TA$  did not differ among agent-host systems or

246 regions, and was determined to best represent average conditions across the study domain.  
247 Effects of modified *TA* were explored in the sensitivity analysis.

248 Following both disturbance types the fraction of vegetation C and N, that is affected by BD, is  
249 transferred into dead organic matter in soil and litter pools at the end of the year of  
250 occurrence. Afterwards C gradually releases from the soil and litter pools to the atmosphere  
251 according to the different decomposition rates for fine litter and coarse woody debris in the  
252 model (Smith *et al.*, 2014). For mortality all tree biomass pools are affected, i.e., C and N in  
253 roots, wood and foliage, while for defoliation only foliage pools are transferred. The amount  
254 of C transferred from live biomass to dead organic matter as a consequence of BDs, called C  
255 flux in the following, is stored separated for the BD types and agents for each year.

256 Disturbances are simulated annually in the following sequence: (1) BD-induced defoliation  
257 (on day 180) – (2) BD-induced mortality – (3) fire – (4) background disturbance (on day  
258 365). In accordance with the data set used, a defoliated tree is not allowed to be killed in the  
259 same year by biotic agents. However, such tree might be killed by fire or background  
260 disturbance at the end of the year defoliation has occurred.

261

## 262 *Simulations and analyses*

263 In a first step, we established a gridded map based on the IDS data and identified tree  
264 mortality and defoliation patterns caused by different BD agents across US forests. These  
265 gridded maps were then applied as fractional disturbances in LPJ-GUESS to simulate BD-  
266 induced C fluxes from live to dead biomass pools, separated by BD types and agents.  
267 Simulations were carried out for all BD-affected grid cells that were covered by climate data  
268 and land use data, resulting in a total of 2009 grid cells with prescribed tree mortality and  
269 1663 grid cells with prescribed defoliation. We also ran the model with a homogeneous BD

270 fraction, i.e., a mean  $D'_f$  applied over all affected grid cells and years, which allowed  
271 assessing the effect of spatio-temporal variability in BD occurrence.

272 To account for potential variations in the BD-related parameters  $TA$  and  $CF$  and to explore  
273 their combined effects on the simulated C fluxes we performed a model sensitivity analysis  
274 where parameter values were modified stepwise. For  $TA$  we tested the potential range of  
275 values between zero and 80 years, i.e., 0-10-20-40-80. The two extreme cases  $TA=0$  and  
276  $TA=80$ , however, are highly unlikely to be an appropriate mean estimate over all kinds of  
277 agent-host systems and environmental conditions covered by this study. For instance,  $TA=0$   
278 would mean that disturbance fractions are equally distributed over all age cohorts, including  
279 saplings – a pattern that is not evident for most BDs. The opposite case  $TA=80$  might be  
280 realistic for some bark beetles (Shore & Safranyik, 1992; cf. Pfeifer *et al.*, 2011), but likely  
281 not for most of the other agents. For the correction factor  $CF$  we used values ranging from  
282 0.02 to 0.3, i.e., 0.02-0.1-0.2-0.3, according to the accuracy of aerial-surveyed polygon data as  
283 previously published. Reported values for bark beetles in the western US range from 0.017 to  
284 0.28 (lower estimate in Meddens *et al.*, 2012 and upper estimate in Hicke *et al.*, 2016,  
285 respectively), with a most realistic mean estimate of  $\sim 0.1$ . Similar factors have also been  
286 applied in a modelling study of insect disturbances in Canada (0.05-0.15; Kurz & Apps,  
287 1999).

288 Finally, the capability of LPJ-GUESS to realistically simulate forest vegetation C pools was  
289 evaluated by comparing simulated above- and belowground living tree C biomass with  
290 observations from the national forest inventory program (FIA, Forest Inventory and Analysis)  
291 conducted by the USDA Forest Service across the conterminous US. Plot-level inventory data  
292 from the years 2000-2009 has already been aggregated to spatially continuous gridded C stock  
293 maps covering the conterminous US with a resolution of 250 m (Wilson *et al.*, 2013). The  
294 spatio-temporal domain of observations well fits to our study domain, with the exception of

295 Alaska where no inventory data was available. We downloaded the two raster maps for  
296 above- and belowground living tree C stocks and aggregated raster size from 250 m to 50 km  
297 by using the ArcGIS Spatial Analyst functionality to facilitate comparability with the LPJ-  
298 GUESS output. Subsequently we merged the above- and belowground C maps to get a total  
299 living tree C stock estimation for each 50 km grid cell. We then overlaid the raster with the  
300 LPJ-GUESS grid containing only those grid cells affected by BDs during the study period,  
301 and applied a spatial join with the grid center points to extract the raster value for each  
302 simulated 0.5° grid cell. This observation-based value was compared to the simulated living  
303 vegetation total C pool, including above- and belowground C, for each BD-affected grid cell  
304 averaged over the years 2000-2009.

305

## 306 **RESULTS**

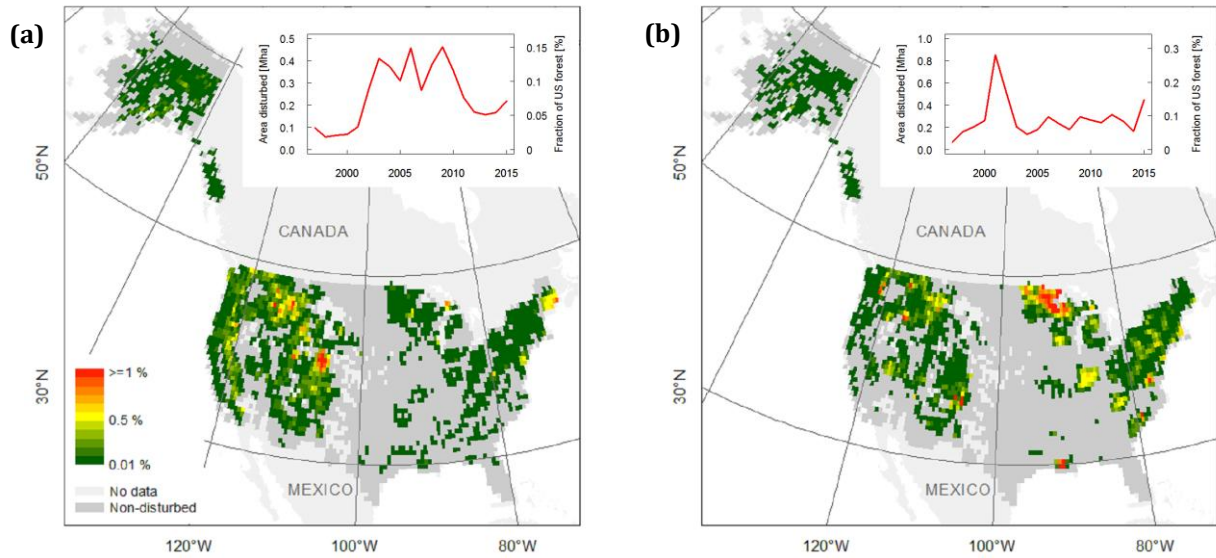
### 307 *Disturbance pattern*

308 IDS reported a total affected area of 46.2 Mha for BD-induced tree mortality, and 52.9 Mha  
309 for defoliation, across US forests over the period 1997-2015. This corresponded to an average  
310 of 2.4 Mha yr<sup>-1</sup> (SD: ±1.3 Mha yr<sup>-1</sup> between years) and 2.8 ±1.7 Mha yr<sup>-1</sup>, respectively.  
311 Following application of the *CF* correction factor of 0.1 nationwide, BD area averaged 0.24  
312 ±0.13 Mha yr<sup>-1</sup> (0.08 ±0.04% yr<sup>-1</sup> of the total US forest cover) for tree mortality and 0.28  
313 ±0.17 Mha yr<sup>-1</sup> (0.09 ±0.06% yr<sup>-1</sup>) for defoliation (Fig. 1 insets). Simulated annual mean BD  
314 fractions  $D'_f$  per grid cell ranged from 0 to 1.3% for mortality ( $n=2009$ , mean  $D'_f=0.08\%$ ), and  
315 from 0 to 1.6% for defoliation ( $n=1663$ , mean  $D'_f=0.1\%$ ; Fig. 1).

316 There were distinct spatial hotspots for both disturbance types with highest mortality fractions  
317 occurring in the mid-western states (Colorado, Wyoming) and notable defoliation in the  
318 north-eastern US (Minnesota, Wisconsin). Temporal trends for both types did not indicate any

319 increase or decrease over the study period, yet disturbance magnitude strongly varied between  
320 years, mainly as a consequence of ephemeral insect and pathogen outbreaks (Fig. 1 insets).  
321 The contribution of different agents varied among BD types, and across space and time (Fig.  
322 2): overall, bark beetles were responsible for most tree mortality and defoliator insects were  
323 the dominant agents causing defoliation, i.e., 72% and 89% of the totals, respectively. Host  
324 types were not equally affected by mortality and defoliation: while (non-lethal) defoliation  
325 disturbed mainly broadleaf trees (51%, with 24% conifers and 25% mixed/unknown),  
326 mortality predominantly befell conifers (77%, with 5% broadleaf and 18%, mixed/unknown).  
327 In the western US and Alaska, tree mortality was principally caused by bark beetles, e.g.,  
328 outbreaks of mountain pine beetle and spruce beetle, with smaller contribution from  
329 pathogens, e.g., causing sudden oak death in California, and other biotic agents. In the eastern  
330 US, all five agent groups contributed more equally to tree mortality, including defoliators,  
331 e.g., eastern spruce budworm, forest tent caterpillar and gypsy moth, and other insects, e.g.,  
332 hemlock and balsam woolly adelgid. In contrast, defoliation –often a trigger of subsequent  
333 tree mortality– was dominantly caused by defoliators across the entire study domain and to  
334 much lesser extent also by other insects and pathogens.





335 **Figure 1.** Biotic disturbance-induced tree mortality (a) and defoliation (b) across US forests  
 336 in 1997-2015. Maps show mean annual disturbance fraction  $D'_f$  (% of forest area) in each  
 337 grid cell as used for simulations; no data = grid cells not covered by forest, climate or land  
 338 use forcing, or located outside the US. Insets indicate temporal trends of annually dissolved  
 339 disturbance area (left axis) and resulting fraction disturbed from total US forest area (right  
 340 axis); note that provided figures are already corrected, i.e., multiplied by a factor of 0.1, to  
 341 convert the affected area to actual disturbed area, and that y-axis scale differs among insets.

342

### 343 **Disturbance-induced C fluxes**

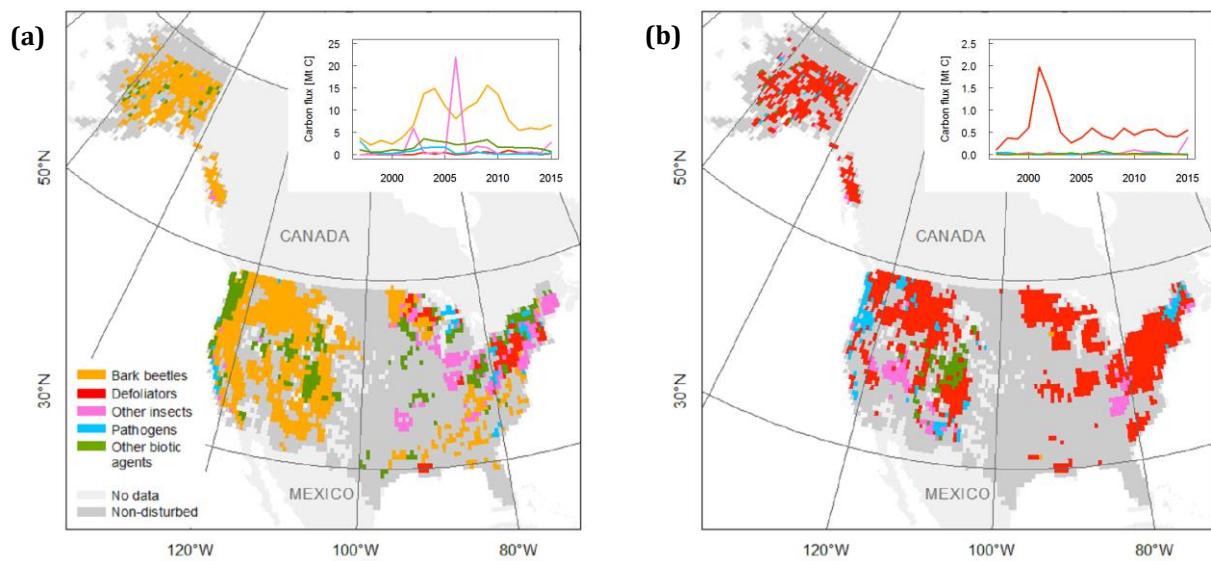
344 The total amount of C transferred from live to dead biomass pools due to BD over the study  
 345 period summed up to 251.6 Mt C, or an annual mean of 13.2 Mt C yr<sup>-1</sup> (SD: ±7.3 Mt C yr<sup>-1</sup>  
 346 between years; Table 2). C fluxes from BD-induced tree mortality were approximately  
 347 twentyfold higher compared to defoliation with a total of 239.5 Mt C (12.6 ±7.3 Mt C yr<sup>-1</sup>)  
 348 and 12.1 Mt C (0.6 ±0.4 Mt C yr<sup>-1</sup>), respectively. Overall, bark beetles impacted the forest C  
 349 cycle most (60.6% of total flux), followed by other insects (14.9%), other biotic agents  
 350 (13.6%), defoliator insects (6.0%) and pathogens (4.9%). That means insect-associated

351 impacts were about five times higher than non-insect agents. Both spatial and temporal C flux  
352 patterns broadly followed those of BD occurrence, exhibiting a notable variability among grid  
353 cells and years, yet without indicating a clear temporal trend (Fig. 3). Highest impacts with  
354 fluxes  $>100 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  occurred in the states of California, Colorado, Washington, Oregon,  
355 Idaho, Montana, Wyoming and Maine, where moderate-to-high mortality fractions coincide  
356 with high simulated tree biomass C density (Fig. 1, 3 and 5). Similar to the BD occurrence,  
357 agent contribution to total fluxes varied among BD types, and across space and time (Fig. 2):  
358 while bark beetles dominated mortality C fluxes in the western states and Alaska with a more  
359 mixed contribution of all groups in the eastern states, defoliator insects most contributed to  
360 defoliation C fluxes over large parts of the US forests.

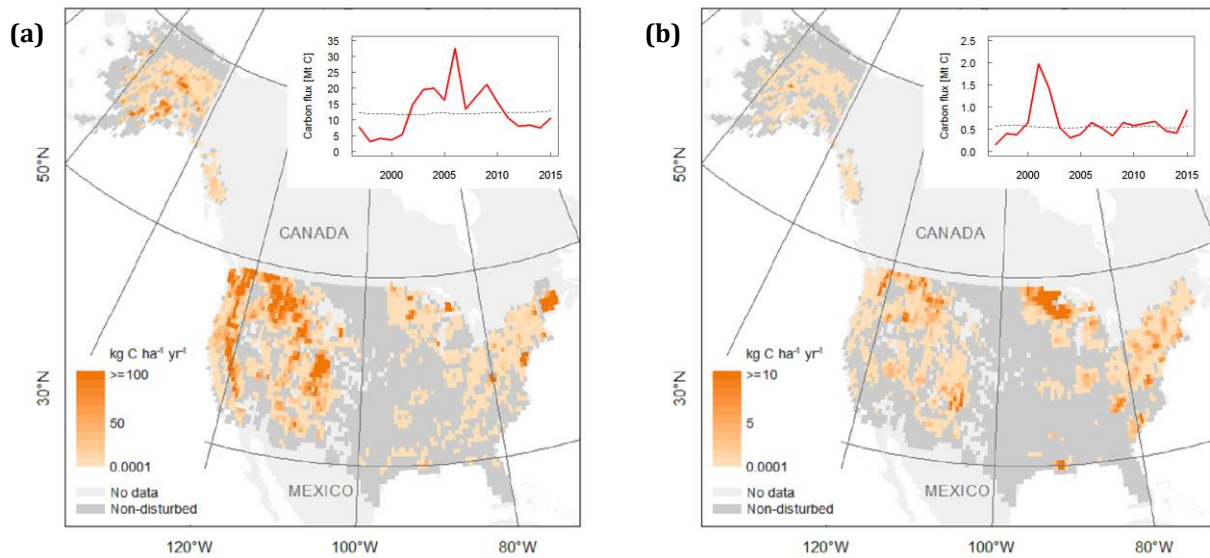
361 The application of a spatio-temporal homogeneous fraction for mortality (mean  $D'_f=0.08\%$ )  
362 and defoliation (mean  $D'_f=0.1\%$ ) resulted in slightly lower total C fluxes, i.e., 96% and 87%,  
363 respectively, compared to the observation-based scenario that considers BD variability across  
364 space and time. Annual deviations between the two scenarios, however, were more  
365 substantial: observation-based fluxes deviated more than  $\pm 20\%$  from the homogeneous  
366 scenario in 16 out of 19 years for mortality and 12 out of 19 years for defoliation (Fig. 3  
367 insets). Hence, applying a constant fraction leads to substantial under-/overestimations for  
368 certain regions and years.

369 **Table 2.** Biotic disturbance-induced carbon flux from live to dead biomass pools for US  
 370 forests in 1997-2015, separated by agents and disturbance types

| Agent group         | Mortality |            | Defoliation |            | Total |            |
|---------------------|-----------|------------|-------------|------------|-------|------------|
|                     | Mt C      | % of total | Mt C        | % of total | Mt C  | % of total |
| Bark beetles        | 152.6     | 63.7       | 0.0         | 0.0        | 152.6 | 60.6       |
| Defoliators         | 4.3       | 1.8        | 10.8        | 89.1       | 15.1  | 6.0        |
| Other insects       | 36.8      | 15.4       | 0.8         | 6.3        | 37.5  | 14.9       |
| Pathogens           | 12.0      | 5.0        | 0.3         | 2.4        | 12.3  | 4.9        |
| Other biotic agents | 34.0      | 14.2       | 0.3         | 2.1        | 34.2  | 13.6       |
| Total               | 239.5     | 100.0      | 12.1        | 100.00     | 251.6 | 100.00     |



371 **Figure 2.** Biotic disturbance agent contribution to tree mortality (a) and defoliation (b)  
 372 across US forests in 1997-2015. Maps show the dominant agent in each grid cell concerning  
 373 both mean disturbance fractions and associated mean carbon fluxes; no data = same as in  
 374 Fig. 1. Insets indicate temporal trends of agent-induced carbon fluxes; line colors refer to  
 375 map legend.



376 **Figure 3.** Biotic disturbance-induced carbon fluxes from live to dead biomass pools through  
 377 tree mortality (a) and defoliation (b) across US forests in 1997-2015. Maps show simulated  
 378 mean annual carbon fluxes ( $\text{kg C ha}^{-1} \text{ yr}^{-1}$ ) in each grid cell; no data = same as in Fig. 1.  
 379 Insets indicate temporal trends with (red solid) and without (black dashed) considering  
 380 spatio-temporal variability of disturbance fractions. Note that scales differ among panels.

381

### 382 **Uncertainty in simulated C fluxes**

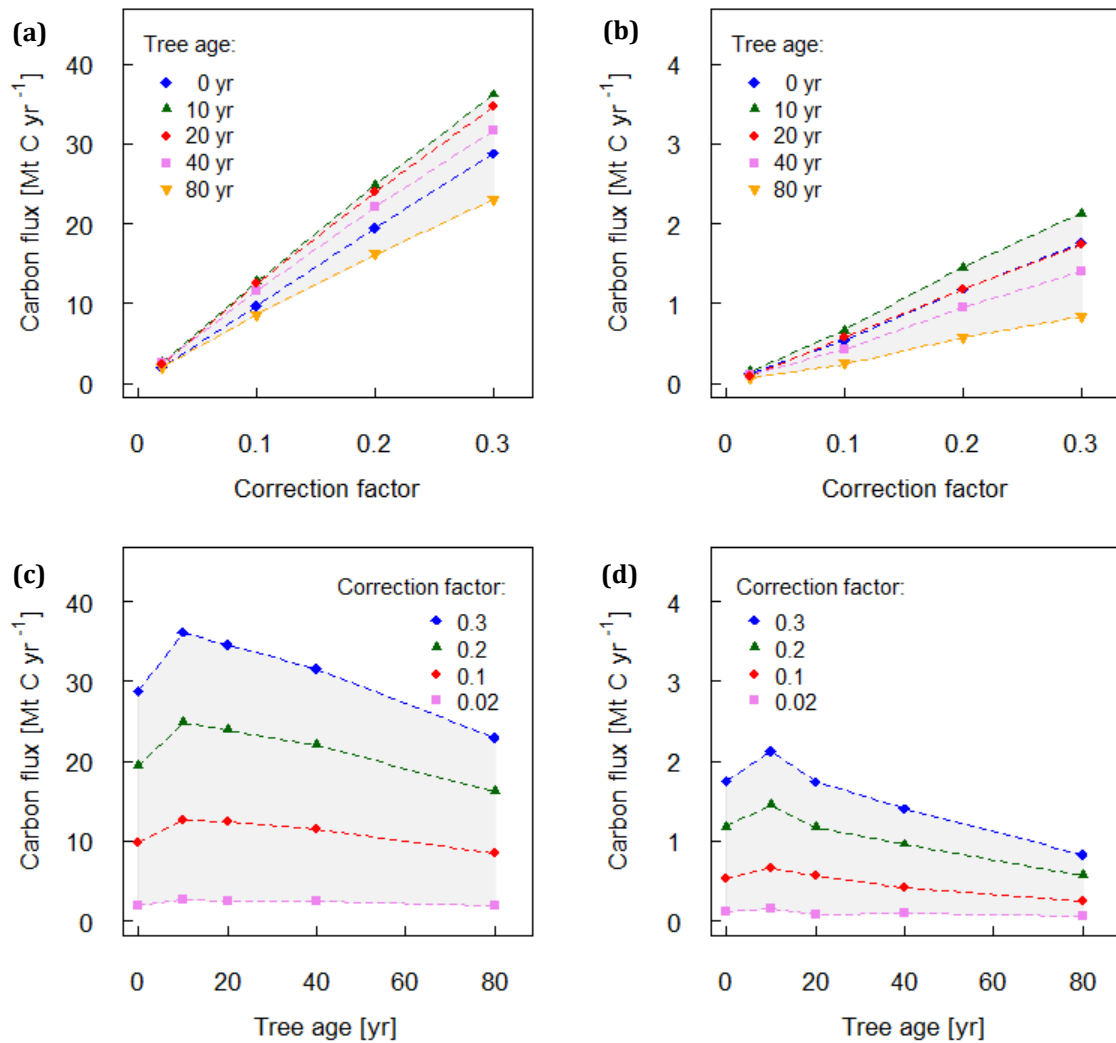
383 Simulated C fluxes through BD-induced tree mortality and defoliation were notably affected  
 384 by both tested parameters, the correction factor  $CF$  and the tree age threshold  $TA$  (Fig. 4). An  
 385 increased  $CF$  resulted in linearly increased C fluxes, a pattern that is mostly independent from  
 386  $TA$  and that is explained by the direct determination of the disturbance fraction  $D'_f$  through  $CF$   
 387 (Fig. 4a,b). In contrast, tree age was less influential for simulated C fluxes and the effect was  
 388 not consistent over the entire range of tested  $TA$ -values: while fluxes increased with tree age  
 389 until  $TA \leq 10$ , they decreased with increasing tree age for  $TA \geq 10$  (Fig. 4c,d). Such negative  
 390 correlation of  $TA$  and C fluxes is counter-intuitive since vegetation C pools typically increase  
 391 with tree age, yet it can be explained by the reduced availability of older susceptible trees to

392 be disturbed in a grid cell. As a result, in grid cells with insufficient older trees simulated  
393 disturbance fractions were lower than originally prescribed, thus leading to a potential  
394 underestimation of C fluxes at higher  $TA$  and in particular under high  $CF$  scenarios.  
395 Nevertheless, our default scenario  $CF=0.1$  was only slightly affected by modified  $TA$ : the  
396 chosen default value of  $TA=20$  provided C fluxes that are robust compared to the entire range  
397 of  $TA$  values tested (red lines in Fig. 4c and d). Overall, our sensitivity experiments suggest  
398 that the presented results based on default settings  $CF=0.1$  and  $TA=20$  provided rather  
399 conservative estimates regarding the range of potential C fluxes of 1.9-36.1 Mt C yr<sup>-1</sup> for tree  
400 mortality (Fig. 4a,c) and 0.1-2.1 Mt C yr<sup>-1</sup> for defoliation (Fig. 4 b,d). The  $CF$  and  $TA$   
401 parameter dependent uncertainty for total BD-induced C fluxes ranged from 38.0 to 725.8 Mt  
402 C, i.e., 2.0-38.2 Mt C yr<sup>-1</sup>.

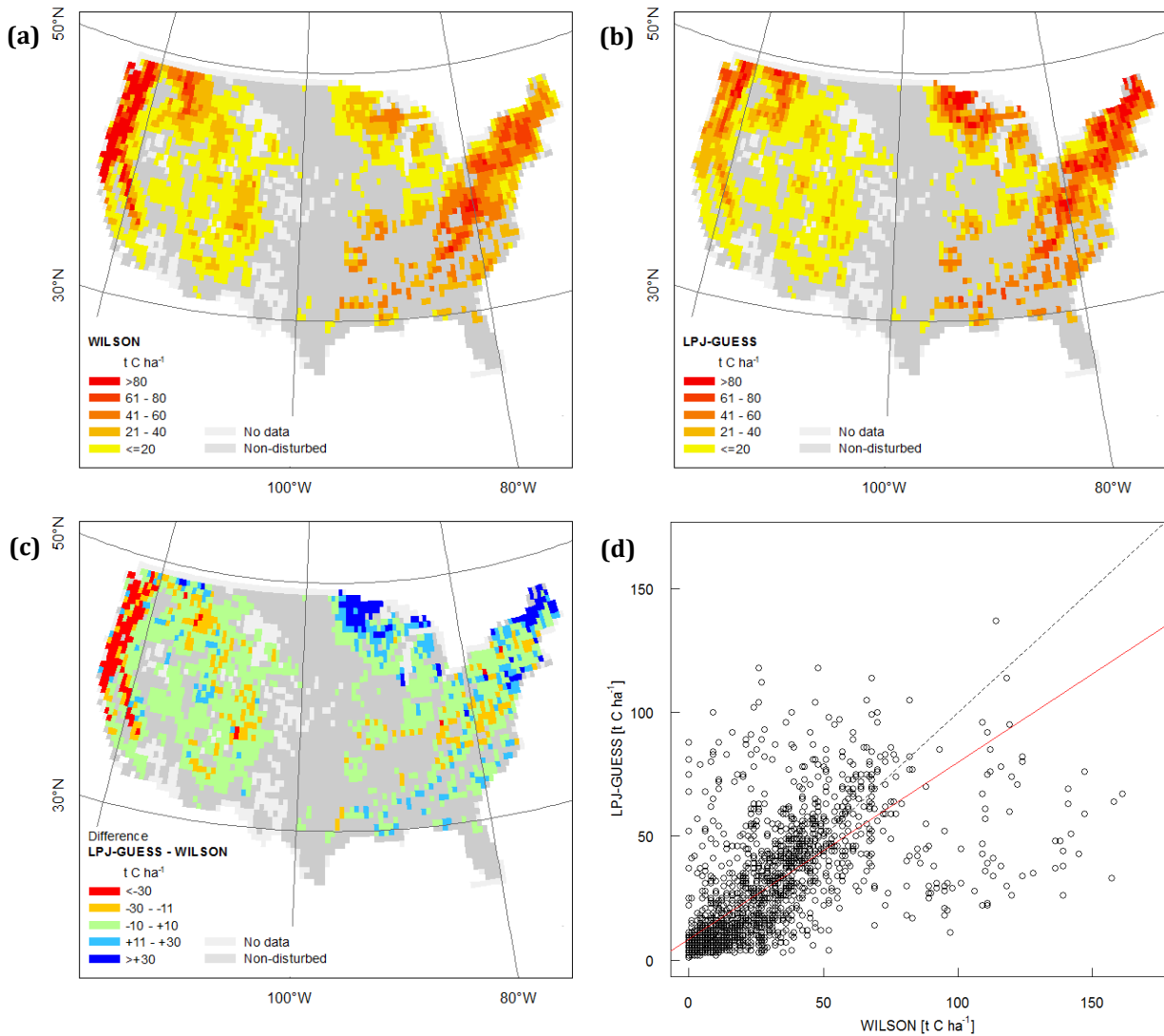
403

#### 404 *Evaluation of simulated vegetation C density*

405 The comparison among observed and simulated C density showed reasonable agreement  
406 regarding the spatial pattern, range and magnitude (Fig. 5). Total mean C density of the  
407 observations ( $29.0 \pm 28.1$  t C ha<sup>-1</sup>) and the model output ( $28.7 \pm 24.0$  t C ha<sup>-1</sup>) for the period  
408 2000-2009 was almost identical over all grid cells affected by BDs across the conterminous  
409 US in 1997-2015 ( $n=1645$ ;  $\pm$ SD indicates between-grid cell variation). Although simulated C  
410 densities were similar to observations over large parts of the US forests, notable deviations  
411 occurred in two regions: LPJ-GUESS underestimates C density in west-coast coniferous  
412 forests, while overestimating it in northeastern mixed forests (Fig. 5c).



413 **Figure 4.** Effect of varying model parameters on biotic disturbance-induced carbon flux from  
 414 live to dead biomass pools through tree mortality (a, c) and defoliation (b, d). Given are mean  
 415 annual carbon fluxes (Mt C yr<sup>-1</sup>) for the period 1997-2015, summed over all disturbed grid  
 416 cells and biotic agents across US forests. Panels (a) and (b) show the modified correction  
 417 factor (CF) on the x-axis, with varying minimum tree age (TA) according to the legend, while  
 418 (c) and (d) provide the opposite perspective. Note that y-axes are different in scale among  
 419 left- and right-hand panels; uncertainty margins are shaded gray.



420 **Figure 5.** Forest vegetation carbon density (mean of years 2000-2009) in grid cells affected  
 421 by biotic disturbances across the conterminous US during the study period 1997-2015  
 422 ( $n=1645$ ): **a)** observations according to Wilson et al. (2013), **b)** LPJ-GUESS model output, **c)**  
 423 difference, and **d)** correlation between simulated and observed carbon density (in red the  
 424 linear fit with  $R^2=0.37$ , the black dashed line represents the 1:1 line; x-axis is truncated for  
 425 clarity).

## 426 **DISCUSSION**

427 By providing the first continental-scale DGVM-based assessment of BD-induced impacts on  
428 forest C cycling, i.e., vegetation C loss, this study contributes to improve our quantitative  
429 understanding beyond the regional scale and single agent-host systems. In particular it allows  
430 for comparisons across regions, BD types and agents. The pronounced C flux variability over  
431 space and time emphasizes the relevance of considering spatio-temporal variability of  
432 disturbances in ecosystem models in order to better explain observed C cycling patterns. Such  
433 consideration will also be important to disentangle the contribution from different  
434 disturbances, e.g., BDs, fire and harvesting, as well as non-disturbance factors, e.g., CO<sub>2</sub>, N  
435 deposition and climate (Zhang *et al.*, 2012; Le Quéré *et al.*, 2016; Williams *et al.*, 2016). Yet,  
436 this finding further calls for intensified forest monitoring efforts to provide BD data at an  
437 adequate resolution, e.g., annually and at sub-national level. To date, accurate assessments of  
438 BD impacts on C cycling are largely impeded by the limited availability and resolution of  
439 such data regarding most of the global forests (Kautz *et al.*, 2017).

440 According to our simulations BD-induced tree mortality and defoliation reduced annual GPP  
441 in forests by an average 21.6 Mt C yr<sup>-1</sup> (0.4% of total), and annual NPP by 5.8 Mt C yr<sup>-1</sup>  
442 (0.3%), when compared to simulations excluding BDs. Likewise, average BD contribution to  
443 total vegetation C turnover time was relatively low, i.e., approximately 3% of the total tree  
444 mortality-caused C flux was due to BDs, and the good performance of LPJ-GUESS in  
445 simulating forest biomass (Fig. 5) gives confidence in the broad magnitude of this outcome. A  
446 similar contribution to turnover has been estimated for the period 1990-2008 in managed  
447 Canadian forests (Stinson *et al.*, 2011). These figures indicate a rather marginal effect of BDs  
448 on C dynamics and forest productivity at the larger spatio-temporal scales, which can be  
449 explained by the low average disturbance fraction (e.g., 0.08% annual mean tree mortality  
450 across our study domain). In contrast, substantial ecosystem response has been shown to



451 occur above a disturbance fraction threshold of approximately 40-60% (Flower & Gonzales-  
452 Meler, 2015; Stuart-Haëntjens *et al.*, 2015), as typically reported for outbreaks temporally  
453 affecting the plot- to landscape scale (e.g., Pfeifer *et al.*, 2011; Hicke *et al.*, 2012; Bright *et*  
454 *al.*, 2013; Flower *et al.*, 2013). For instance, NPP was reduced by 31% due to emerald ash  
455 borer-caused tree mortality across 45 sample plots over a 7-year period in Ohio (Flower *et al.*,  
456 2013), and aboveground tree C stocks were reduced by 40-50% in a severely bark beetle-  
457 disturbed landscape over a 8-year period in Idaho (Bright *et al.*, 2013; see also Hicke *et al.*,  
458 2012 for additional examples).

459 Recent C flux estimates due to BD-induced tree mortality across US forests largely varied in  
460 magnitude, mainly because they were based on different data sets for vegetation C pools and  
461 mortality fractions. For instance, previous assessments on bark beetle-induced C fluxes  
462 through tree mortality in the western US have been reported 20.6 Mt C yr<sup>-1</sup>, with a range of  
463 estimates 1.8-24.4 Mt C yr<sup>-1</sup>, for the period 1997-2010 (Hicke *et al.*, 2013), 4.6-15.4 Mt C yr<sup>-1</sup>  
464 for 2000-2009 (Ghimire *et al.*, 2015), and 14.6 ±7.0 Mt C yr<sup>-1</sup> for 2003-2013 (aboveground C  
465 only; Berner *et al.*, 2017). By comparison, we estimated fluxes of 7.0 Mt C yr<sup>-1</sup> – with a  
466 potential range of 1.1-19.2 Mt C yr<sup>-1</sup> according to our sensitivity experiments – due to tree  
467 mortality caused by western bark beetles over the study period 1997-2015. Note that this  
468 figure is a conservative estimate as it excludes multi-agent BDs where bark beetles were  
469 involved but were not categorized as the sole causal agent in the IDS (e.g., pinyon pine  
470 mortality in the ‘other biotic agents’ category). A northern hemisphere-wide assessment  
471 resulted in total mortality-induced C fluxes due to BDs in US forests to be three times larger  
472 than the 12.6 Mt C yr<sup>-1</sup> calculated here (37.1 Mt C yr<sup>-1</sup> for 1997-2013; Kautz *et al.*, 2017).  
473 Those C amounts, however, were calculated at an aggregated spatial resolution only (e.g., not  
474 merging disturbance polygons at 0.5° grid cell-level) and were based on less detailed global  
475 biomass C data.

476 Though the comparison with an observation-based C density map (Wilson *et al.*, 2013)  
477 demonstrated our simulated C density to be reliable over the vast majority of grid cells, LPJ-  
478 GUESS over-/underestimated C density locally (Fig. 5c). This leads to potentially  
479 overestimated C fluxes in parts of the northeastern US, while C fluxes are most likely  
480 underestimated in west-coast forests. We should note that the representation of C cycle  
481 processes, e.g., photosynthesis and respiration of trees, is highly sensitive to model-specific  
482 parameters and may differ among DGVMs (Zaehle *et al.*, 2005; Pappas *et al.*, 2013; Piao *et*  
483 *al.*, 2013); hence the application of our approach within other models may likely increase  
484 uncertainty in BD-induced C fluxes.

485 Applied BD fractions were based on the aerial-surveyed IDS polygons and corrected  
486 ( $CF=0.1$ ) in order to obtain the actual disturbed area. Nevertheless such generic factor  
487 averaged across US forests is an oversimplification since polygon accuracy and disturbance  
488 severity may widely differ, e.g., due to different detectability across forest types and different  
489 cooperating agencies responsible for data acquisition (Johnson & Wittwer, 2008). Prominent  
490 peaks of BD occurrence and associated C fluxes (e.g., 2001-2002 forest tent caterpillar, 2006  
491 hemlock woolly adelgid; Fig. 1-3) are most likely overestimated because of a very rough  
492 delineation of disturbance polygons. In contrast, for other parts of the study domain with high  
493 survey accuracy the corrected fractions might underestimate true disturbance occurrence and  
494 fluxes. Not surprisingly, the correction factor has a large influence on C fluxes as it directly  
495 determines the area affected by mortality or defoliation in the model (Fig. 4). Since aerial  
496 surveys were not capable to cover the complete US forest area consistently over the study  
497 period, calculated BD fractions and associated C fluxes might be underestimated for those  
498 areas not being surveyed regularly, such as remote forests in Alaska. Improvements on BD  
499 data coverage and accuracy, in combination with reliable tree biomass C maps, would help  
500 reducing uncertainty regarding BD-induced C fluxes (Berner *et al.*, 2017). Remote sensing

501 approaches, for instance, might facilitate a spatially-extended and nearly tree-resolving  
502 detection in the future, thereby providing more complete and accurate metrics on forest area  
503 killed or defoliated.

504 Among the natural disturbance regimes occurring across US forests, BDs, windthrow and fire  
505 are recognized as the ones most affecting C cycling, despite differences concerning spatial  
506 patterns and temporal variability (Zhang *et al.*, 2012; Hicke *et al.*, 2013; Williams *et al.*,  
507 2016). Regionally, the magnitude of tree mortality and associated C fluxes due to western  
508 bark beetles has been shown to be similar to fire impacts over recent decades (Hicke *et al.*,  
509 2013; Ghimire *et al.*, 2012, 2015), or even exceeded them (Berner *et al.*, 2017). Accordingly  
510 for the continuous US we estimated total BD-induced tree mortality C fluxes to be slightly  
511 higher ( $11.4 \pm 7.1 \text{ Mt C yr}^{-1}$ ) compared to forest fire emissions reported over the same period  
512 1997-2015 ( $7.8 \pm 3.9 \text{ Mt C yr}^{-1}$ , van der Werf *et al.*, 2017). A direct comparison of C fluxes  
513 between BDs and fire, however, is impeded by varying C dynamics: large parts of fire-caused  
514 C fluxes are immediately directed to the atmosphere via combustion, while C is more  
515 gradually released from dead organic matter pools to the atmosphere as dead matter decays  
516 following BDs. The period of decomposition processes typically spans from months (leaves,  
517 fine roots) to decades (snags), depending on environmental conditions and the affected tree  
518 species (Edburg *et al.*, 2011; Hilger *et al.*, 2012; Landry *et al.*, 2016). Hence, C fluxes  
519 reported in this study can be understood as committed rather than direct C transfers from  
520 living biomass to the atmosphere. Possible interactions between fire and BDs (e.g., fire-  
521 scorched trees increase susceptibility to BDs, or vice versa, BD-induced increase in fuel load  
522 enhances fire probability), or windthrow and BDs (e.g., windthrown trees provide abundant  
523 breeding material for bark beetle population growth) were not explored in this study;  
524 nevertheless, such disturbance feedbacks in combination with different management strategies  
525 may provide fruitful subjects for further research.

526 In contrast to disturbances like fire or windthrow, a process-based representation of BDs in  
527 large-scale ecosystem models such as DGVMs is particularly challenging due to the huge  
528 diversity of processes involved, e.g., concerning reproduction, development, mortality,  
529 dispersal and attack behavior of BD agents. Each of these processes largely depends on the  
530 specific agent-host system, i.e., it differs among species, and also on the environmental  
531 conditions that may vary across space and time. Future climatic changes are expected to  
532 differentially affect processes and agent guilds (Weed *et al.*, 2013; Kolb *et al.*, 2016).  
533 Moreover, stochasticity is a particularly strong factor determining BD occurrence (Sharma *et*  
534 *al.*, 2015), e.g., through dispersal, climate-sensitive population build-up, or when invasive  
535 species are accidentally introduced. This complexity complicates a prognostic modelling  
536 approach based on a few climatic and ecosystem-specific parameters as has been carried out  
537 for fire (Hantson *et al.*, 2016) and windthrow disturbances (Lagergren *et al.*, 2012). Coupling  
538 a DGVM with a BD agent population model, that explicitly simulates most if not all of the  
539 relevant processes, has been shown feasible for single agent-host systems where the necessary  
540 data is available (e.g., Jönsson *et al.*, 2012; Temperli *et al.*, 2013; Seidl & Rammer, 2017; see  
541 also S1). However, in regional to global applications comprising numerous agents, the  
542 challenge of parametrization with such detail requires extensive generalization.

543 One simplifying step, followed here, avoids process-based simulation of agent population  
544 dynamics by prescribing disturbance fractions, implicitly considering agent population  
545 dynamics and spatial interaction between grid cells. The representation of BDs is thus rather  
546 similar to accounting for human-induced disturbances such as variable land use. In contrast to  
547 previous DGVM- or FLM-based studies (S1), we used a simple functional type-like approach  
548 that distinguishes between two major BD types, tree mortality and defoliation, across specific  
549 agent-host systems. These types broadly integrate over diverse disturbance mechanisms  
550 affecting tree physiology, e.g., growth, water use or C allocation. Similar to the concept of

551 PFTs, functional BD types help reducing agent and process diversity while considering  
552 differential impacts on tree physiology (Dietze & Matthes, 2014; Landry *et al.*, 2016). Our  
553 approach particularly enables large-scale applications, up to the global scale, as it is not *a*  
554 *priori* constrained by species-specific parameters and processes. Furthermore, it allows the  
555 simultaneous simulation of tree mortality and defoliation by any kind of BD agent (insects,  
556 pathogens, others), including many-to-many agent-host relations, and thus facilitates a holistic  
557 representation of different BD regimes occurring in the same spatio-temporal domain.  
558 Consequently, this leads to a more realistic simulation of large-scale forest ecosystem  
559 dynamics compared to previous modelling approaches. The extension is principally applicable  
560 irrespective of the spatial scale, time period or disturbance agent studied, with the level of  
561 detail being adjustable according to the available input data and specific research questions.  
562 For instance, overall BD-induced tree mortality and/or defoliation fractions can be used when  
563 agent-separated fractions are absent as is the case for most of the globe (Kautz *et al.*, 2017), or  
564 the extension can be applied at species level, e.g., for agent species that are of particular  
565 interest such as the mountain pine beetle, if the data is provided accordingly. Overall, these  
566 features provide a substantial improvement over the current state of neglecting BDs at the  
567 large scale.

568 Despite given differences in model parametrization and structure the presented approach may  
569 serve as a blueprint for other DGVMs or similar models with potential for further  
570 development and adaption, e.g., regarding (i) the variation of BD-related parameters *CF* and  
571 *TA* according to the agent-host systems investigated, (ii) additional host specifying factors,  
572 such as considering single species or temporal drought stress, (iii) the implementation of snag  
573 dynamics that account for delayed C and N fluxes, and (iv) the capacity of the tree to reflush  
574 within-season following defoliation. Future disturbance trajectories can be simulated by  
575 modifying disturbance fractions, e.g., altered fractions or shifted ranges as projected for some

576 bark beetles in the US as a consequence of climate warming (Bentz *et al.*, 2010). Ultimately,  
577 however, process-based representation of BDs – though it is challenging – needs to be refined  
578 in the next-generation of DGVMs, thereby enabling the simulation of dynamic feedbacks  
579 between CO<sub>2</sub>, climate, vegetation and disturbances, as well as of interactions between  
580 different disturbances, and interactions between disturbances and forest management.

581

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589 the U.S. Government. This is paper number 31 of the Birmingham Institute of Forest  
590 Research.

591

## 592 **SUPPLEMENTARY INFORMATION**

593 **S1 Review of biotic forest disturbance representation in large-scale, process-**  
594 **based ecosystem models**

595

## 596 **REFERENCES**

597 Anderegg WRL, Martinez-Vilalta J, Cailleret M, Camarero JJ, Ewers BE, Galbraith D,  
598 Gessler A, Grote R, Huang C, Levick SR, Powell TL, Rowland L, Sánchez-Salguero R,  
599 Trotsiuk V (2016) When a tree dies in the forest: scaling climate-driven tree mortality to  
600 ecosystem water and carbon fluxes. *Ecosystems*, **19**, 1133–1147.

601 Arneth A, Niinemets Ü (2010) Induced BVOCs: how to bug our models? *Trends in Plant*  
602 *Science*, **15**, 118–125.

603 Bartholomé E, Belward AS (2005) GLC2000: a new approach to global land cover mapping  
604 from Earth observation data. *International Journal of Remote Sensing*, **26**, 1959–1977.

605 Battisti C, Poeta G, Fanelli G (2016) *An introduction to disturbance ecology*. Springer Nature,  
606 Switzerland, 178 p.

607 Bayer AD, Lindeskog M, Pugh TAM, Anthoni PM, Fuchs R, Arneth A (2017) Uncertainties  
608 in the land-use flux resulting from land-use change reconstructions and gross land transitions.  
609 *Earth System Dynamics*, **8**, 91–111.

610 Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF,  
611 Seybold SJ (2010) Climate change and bark beetles of the western United States and Canada:  
612 direct and indirect effects. *Bioscience*, **60**, 602–613.

613 Berg AR, Heald CL, Huff Hartz KE, Hallar AG, Meddens AJH, Hicke JA5, Lamarque J-F,  
614 Tilmes S (2013) The impact of bark beetle infestations on monoterpene emissions and  
615 secondary organic aerosol formation in western North America. *Atmospheric Chemistry and*  
616 *Physics*, **13**, 3149–3161.

617 Berner LT, Law BE, Meddens AJH, Hicke JA (2017) Tree mortality from fires, bark beetles,  
618 and timber harvest during a hot and dry decade in the western United States (2003-2012).  
619 *Environmental Research Letters*, **12**, 065005.

620 Boyd IL, Freer-Smith PH, Gilligan CA, Godfray HCJ (2013) The consequences of tree pests  
621 and diseases for ecosystem services. *Science*, **342**, 1235773.

622 Bright BC, Hicke JA, Meddens AJH (2013) Effects of bark beetle-caused tree mortality on  
623 biogeochemical and biogeophysical MODIS products. *Journal of Geophysical Research:*  
624 *Biogeosciences*, **118**, 974–982.

625 Brown MG, Black TA, Nestic Z, Fredeen AL, Foord VN, Spittlehouse DL, Bowler R, Burton  
626 PJ, Trofymow JA, Grant NJ, Lessard D (2012) The carbon balance of two lodgepole pine  
627 stands recovering from mountain pine beetle attack in British Columbia. *Agricultural and*  
628 *Forest Meteorology*, **153**, 82–93.

629 Canadian Forest Service (2017) *National Forestry Database*. Available at  
630 <http://nfdp.ccfm.org>, assessed 2017-03-23.

631 Chen F, Zhang G, Barlage M, Zhang Y, Hicke JA, Meddens A, Zhou G, Massman WJ, Frank  
632 J (2015) An observational and modeling study of impacts of bark beetle-caused tree mortality  
633 on surface energy and hydrological cycles. *Journal of Hydrometeorology*, **16**, 744–761.

634 Clark KL, Skowronski N, Hom J (2010) Invasive insects impact forest carbon dynamics.  
635 *Global Change Biology*, **16**, 88–101.

636 Cooper LA, Ballantyne AP, Holden ZA, Landguth EL (2017) Disturbance impacts on land  
637 surface temperature and gross primary productivity in the western United States. *Journal of*  
638 *Geophysical Research: Biogeosciences*, **122**, 930–946.

639 Costilow KC, Knight KS, Flower CE (2017) Disturbance severity and canopy position control  
640 the radial growth response of maple trees (*Acer* spp.) in forests of northwest Ohio impacted  
641 by emerald ash borer (*Agrilus planipennis*). *Annals of Forest Science*, **74**, 10. Crowley KF,  
642 Lovett GM, Arthur MA, Weathers KC (2016) Long-term effects of pest-induced tree species



643 change on carbon and nitrogen cycling in northeastern U.S. forests: A modeling analysis.  
644 *Forest Ecology and Management*, **372**, 269–290.

645 Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Hanson PJ, Irland  
646 LC, Lugo AE, Peterson CJ, Simberloff D, Swanson FJ, Stocks BJ, Wotton BM (2001)  
647 Climate change and forest disturbances. *BioScience*, **51**, 723–734.

648 De Jager NR, Drohan PJ, Miranda BM, Sturtevant BR, Stout SL, Royo AA, Gustafson EJ,  
649 Romanski MC (2017) Simulating ungulate herbivory across forest landscapes: A  
650 browsing extension for LANDIS-II. *Ecological Modelling*, **350**, 11–29.

651 Dietze MC, Matthes JH (2014) A general ecophysiological framework for modelling the  
652 impact of pests and pathogens on forest ecosystems. *Ecological Letters*, **17**, 1418–1426.

653 Duhl TR, Gochis D, Guenther A, Ferrenberg S, Pendall E (2013) Emissions of BVOC from  
654 lodgepole pine in response to mountain pine beetle attack in high and low mortality forest  
655 stands. *Biogeosciences*, **10**, 483–499.

656 Dymond CC, Neilson ET, Stinson G, Porter K, MacLean DA, Gray DR, Campagna M, Kurz  
657 WA (2010) Future spruce budworm outbreak may create a carbon source in eastern Canadian  
658 forests. *Ecosystems*, **13**, 917–931.

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

662 Edburg SL, Hicke JA, Brooks PD, Pendall EG, Ewers BE, Norton U, Gochis D, Gutmann  
663 ED, Meddens AJH (2012) Cascading impacts of bark beetle-caused tree mortality on coupled  
664 biogeophysical and biogeochemical processes. *Frontiers in Ecology and the Environment*, **10**,  
665 416–424.

666 Fisher JB, Huntzinger DN, Schwalm CR, Sitch S (2014) Modeling the terrestrial biosphere.  
667 *Annual Review of Environment and Resources*, **39**, 91–123.

668 Flower CE, Gonzales-Meler MA (2015) Responses of temperate forest productivity to insect  
669 and pathogen disturbances. *Annual Review of Plant Biology*, **66**, 547–569.

670 Flower CE, Knight KS, Gonzalez-Meler MA (2013) Impacts of the emerald ash borer  
671 (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon  
672 cycling and successional dynamics in the eastern United States. *Biological Invasions*, **15**,  
673 931–944.

674 Ghimire B, Williams CA, Collatz GJ, Vanderhoof M (2012) Fire-induced carbon emissions  
675 and regrowth uptake in western U.S. forests: documenting variation across forest types, fire  
676 severity, and climate regions. *Journal of Geophysical Research: Biogeosciences*, **117**,  
677 G03036.

678 Ghimire B, Williams CA, Collatz GJ, Vanderhoof M, Rogan J, Kulakowski D, Masek JG  
679 (2015) Large carbon release legacy from bark beetle outbreaks across Western United States.  
680 *Global Change Biology*, **21**, 3087–3101.

681 Hansen EM, Michaels Goheen E (2000) *Phellinus weirii* and other native root pathogens as  
682 determinants of forest structure and process in western North America. *Annual Review of*  
683 *Phytopathology*, **38**, 515–539.

684 Hantson S, Arneth A, Harrison SP, Kelley DI, Prentice IC, Rabin SS, Archibald S, Mouillot  
685 F, Arnold SR, Artaxo P, Bachelet D, Ciais P, Forrest M, Friedlingstein P, Hickler T, Kaplan  
686 JO, Kloster S, Knorr W, Lasslop G, Li F, Mangeon S, Melton JR, Meyn A, Sitch S, Spessa A,  
687 van der Werf GR, Voulgarakis A, Yue C (2016) The status and challenge of global fire  
688 modelling. *Biogeosciences*, **13**, 3359–3375.

689 Hawkins CDB, Dhar A, Balliet NA, Runzer KD (2012) Residual mature trees and secondary  
690 stand structure after mountain pine beetle attack in central British Columbia. *Forest Ecology*  
691 *and Management*, **277**, 107–115.

692 Hicke JA, Allen CD, Desai AR, Dietze MC, Hall RJ, Hogg EH, Kashian DM, Moore D, Raffa  
693 KF, Sturrock RN, Vogelmann J (2012) Effects of biotic disturbances on forest carbon cycling  
694 in the United States and Canada. *Global Change Biology*, **18**, 7–34.

695 Hicke JA, Jenkins JC (2008) Mapping lodgepole pine stand structure susceptibility to  
696 mountain pine beetle attack across the western United States. *Forest Ecology and*  
697 *Management*, **255**, 1536–1547.

698 Hicke JA, Meddens AJH, Allen CD, Kolden CA (2013) Carbon stocks of trees killed by bark  
699 beetles and wildfire in the western United States. *Environmental Research Letters*, **8**, 035032.

700 Hicke JA, Meddens AJH, Kolden C (2016) Recent tree mortality in the western United States  
701 from bark beetles and forest fire. *Forest Science*, **62**, 141–153.

702 Hilger AB, Shaw CH, Metsaranta JM, Kurz WA (2012) Estimation of snag carbon transfer  
703 rates by ecozone and lead species for forests in Canada. *Ecological Applications*, **22**, 2078–  
704 2090.

705 Hurtt G, Chini L, Frolking S, Sahajpal R (2016) Land Use Harmonization 2. Available at:  
706 <http://luh.umd.edu/data.shtml>, version LUH2 v2h from 2016-12-14, accessed 2017-03-23.

707 Johnson E, Wittwer D (2008) Aerial detection surveys in the United States. *Australian*  
708 *Forestry*, **71**, 212–215.

709 Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC,  
710 Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing

711 disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and*  
712 *Environment*, **14**, 369–378.

713 Jönsson AM, Schroeder LM, Lagergren F, Anderbrant O, Smith B (2012) Guess the impact of  
714 *Ips typographus* – an ecosystem modelling approach for simulating spruce bark beetle  
715 outbreaks. *Agricultural and Forest Meteorology*, **166**, 188–200.

716 Kautz M, Meddens AJH, Hall RJ, Arneeth A (2017) Biotic disturbances in Northern  
717 Hemisphere forests – a synthesis of recent data, uncertainties and implications for forest  
718 monitoring and modelling. *Global Ecology and Biogeography*, **26**, 533–552.

719 Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS  
720 (2016) Observed and anticipated impacts of drought on forest insects and pathogens in the  
721 United States. *Forest Ecology and Management*, **380**, 321–334.

722 Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian  
723 forest sector. *Ecological Applications*, **9**, 526–547.

724 Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Ebata T, Safranyik  
725 L (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**,  
726 987–990.

727 Lagergren F, Jönsson AM, Blennow K, Smith B (2012) Implementing storm damage in a  
728 dynamic vegetation model for regional applications in Sweden. *Ecological Modelling*, **247**,  
729 71–82.

730 Landry J-S, Price DT, Ramankutty N, Parrott L, Matthews HD (2016) Implementation of a  
731 Marauding Insect Module (MIM, version 1.0) in the Integrated Biosphere Simulator (IBIS,  
732 version 2.6b4) dynamic vegetation–land surface model. *Geoscientific Model Development*, **9**,  
733 1243–1261.

734 Le Quéré C, Andrew RM, Canadell JG, Sitch S, Korsbakken JI, Peters GP, Manning AC,  
735 Boden TA, Tans PP, Houghton RA, Keeling RF, Alin S, Andrews OD, Anthoni P, Barbero L,  
736 Bopp L, Chevallier F, Chini LP, Ciais P, Currie K, Delire C, Doney SC, Friedlingstein P,  
737 Gkritzalis T, Harris I, Hauck J, Haverd V, Hoppema M, Klein Goldewijk K, Jain AK, Kato E,  
738 Körtzinger A, Landschützer P, Lefèvre N, Lenton A, Lienert S, Melton JR, Metzl N, Millero  
739 F, Monteiro PMS, Munro DR, Nabel JEMS, Nakaoka S-I, O'Brien K, Olsen A, Omar AM,  
740 Ono T, Pierrot D, Poulter B, Rödenbeck C, Salisbury J, Schuster U, Schwinger J, Séférian R,  
741 Skjelvan I, Stocker BD, Sutton AJ, Takahashi T, Tian H, Tilbrook B, van der Laan-Luijkx IT,  
742 van der Werf GR, Viovy N, Walker AP, Wiltshire AJ, Zaehle S (2016) Global carbon budget  
743 2016. *Earth System Science Data*, **8**, 605–649.

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

747 Malmström CM, Raffa KF (2000) Biotic disturbance agents in the boreal forest:  
748 considerations for vegetation change models. *Global Change Biology*, **6**, 35–48.

749 Meddens AJH, Hicke JA, Ferguson CA (2012) Spatiotemporal patterns of observed bark  
750 beetle-caused tree mortality in British Columbia and the western United States. *Ecological*  
751 *Applications*, **22**, 1876–1891.

752 Medvigy D, Clark KL, Skowronski NS, Schäfer KVR (2012) Simulated impacts of insect  
753 defoliation on forest carbon dynamics. *Environmental Research Letters*, **7**, 045703.

754 Pappas C, Fatichi S, Leuzinger S, Wolf A, Burlando P (2013) Sensitivity analysis of a  
755 process-based ecosystem model: Pinpointing parameterization and structural issues. *Journal*  
756 *of Geophysical Research: Biogeosciences*, **118**, 505–528.

757 Pfeifer EM, Hicke JA, Meddens AJH (2011) Observations and modeling of aboveground tree  
758 carbon stocks and fluxes following a bark beetle outbreak in the western United States.  
759 *Global Change Biology*, **17**, 339–350.

760 Piao S, Sitch S, Ciais P, Friedlingstein P, Peylin P, Wang X, Ahlström A, Anav A, Canadell  
761 JG, Cong N, Huntingford C, Jung M, Levis S, Levy PE, Li J, Lin X, Lomas MR, Lu M, Luo  
762 Y, Ma Y, Myneni RB, Poulter B, Sun Z, Wang T, Viovy N, Zaehle S, Zeng N (2013)  
763 Evaluation of terrestrial carbon cycle models for their response to climate variability and to  
764 CO<sub>2</sub> trends. *Global Change Biology*, **19**, 2117–2132.

765 Quillet A, Peng C, Garneau M (2010) Toward dynamic global vegetation models for  
766 simulating vegetation-climate interactions and feedbacks: recent developments, limitations,  
767 and future challenges. *Environmental Reviews*, **18**, 333–353.

768 Running SW (2008) Ecosystem disturbance, carbon, and climate. *Science*, **321**, 652–653.

769 Schäfer KVR, Clark KL, Skowronski N, Hamerlynck EP (2010) Impact of insect defoliation  
770 on forest carbon balance as assessed with a canopy assimilation model. *Global Change*  
771 *Biology*, **16**, 546–560.

772 Seidl R, Rammer W (2017) Climate change amplifies the interactions between wind and bark  
773 beetle disturbances in forest landscapes. *Landscape Ecology*, **32**, 1485–1498.

774 Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D,  
775 Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA,  
776 Reyer CPO (2017) Forest disturbances under climate change. *Nature Climate Change*, **7**,  
777 395–402.

778 Sharma Y, Abbott KC, Dutta PS, Gupta AK (2015) Stochasticity and bistability in insect  
779 outbreak dynamics. *Theoretical Ecology*, **8**, 163–174.

780 Shore TL, Safranyik L (1992) Susceptibility and risk rating systems for the mountain pine  
781 beetle in lodgepole pine stands. *Information report*, BC-X-336, Forestry Canada, Pacific  
782 Forestry Centre, Victoria, BC, 12 p.

783 Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the  
784 modelling of terrestrial ecosystems: comparing two contrasting approaches within European  
785 climate space. *Global Ecology and Biogeography*, **10**, 621–637.

786 Smith B, Wårlind D, Arneth A, Hickler T, Leadley P, Siltberg J, Zaehle S (2014) Implications  
787 of incorporating N cycling and N limitations on primary production in an individual-based  
788 dynamic vegetation model. *Biogeosciences*, **11**, 2027–2054.

789 Stinson G, Kurz WA, Smyth CE, Neilson ET, Dymond CC, Metsaranta JM, Boisvenue C,  
790 Rampley GJ, Li Q, White TM, Blain D (2011) An inventory-based analysis of Canada's  
791 managed forest carbon dynamics, 1990 to 2008. *Global Change Biology*, **17**, 2227–2244.

792 Stuart-Haëntjens EJ, Curtis PS, Fahey RT, Vogel CS, Gough CM (2015) Net primary  
793 production of a temperate deciduous forest exhibits a threshold response to increasing  
794 disturbance severity. *Ecology*, **96**, 2478–2487.

795 Temperli C, Veblen TT, Hart SJ, Kulakowski D, Tepley AJ (2015) Interactions among spruce  
796 bark beetle disturbances, climate change and forest dynamics captured by a forest landscape  
797 model. *Ecosphere*, **6**, 231.

798 Thom D, Seidl R (2016) Natural disturbance impacts on ecosystem services and biodiversity  
799 in temperate and boreal forests. *Biological Review*, **91**, 760–781.

800 Thonicke K, Venevsky S, Sitch S, Cramer W (2001) The role of fire disturbance for global  
801 vegetation dynamics: coupling fire into a dynamic global vegetation model. *Global Ecology  
802 and Biogeography*, **10**, 661–677.

803 Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology*, **91**,  
804 2833–2849.

805 USDA Forest Service (2005) *Aerial Survey Geographic Information System Handbook*.  
806 United States Department of Agriculture, Washington, DC, 35 p. Available at:  
807 [https://www.fs.fed.us/foresthealth/technology/ads\\_standards.shtml](https://www.fs.fed.us/foresthealth/technology/ads_standards.shtml), assessed 2017-03-23.

808 USDA Forest Service (2017) *Insect and disease survey data base*. Available at:  
809 <http://foresthealth.fs.usda.gov>, assessed 2017-03-23.

810 van der Werf GR, Randerson JT, Giglio L, van Leeuwen TT, Chen Y, Rogers BM, Mu M,  
811 van Marle MJE, Morton DC, Collatz GJ, Yokelson RJ, Kasibhatla PS (2017) Global fire  
812 emissions estimates during 1997–2016. *Earth System Science Data*, **9**, 697–720. Data  
813 available at: <http://www.globalfiredata.org/data.html>, assessed 2017-05-07.

814 van Lierop P, Lindquist E, Sathyapala S, Franceschini G (2015) Global forest area  
815 disturbance from fire, insect pests, diseases and severe weather events. *Forest Ecology and*  
816 *Management*, **352**, 78–88.

817 Weed AS, Ayres MP, Hicke JA (2013) Consequences of climate change for biotic  
818 disturbances in North American forests. *Ecological Monographs*, **83**, 441–470.

819 Williams C, Gu H, MacLean R, Masek J, Collatz G (2016) Disturbance and the carbon  
820 balance of US forests: A quantitative review of impacts from harvests, fires, insects, and  
821 droughts. *Global and Planetary Change*, **143**, 66–80.

822 Wilson BT, Woodall CW, Griffith DM (2013) Imputing forest carbon stock estimates from  
823 inventory plots to a nationally continuous coverage. *Carbon Balance and Management*, **8**:1.  
824 Data available at: <http://dx.doi.org/10.2737/RDS-2013-0004>, assessed 2017-03-23.



- 825 Zaehle S, Sitch S, Smith B, Hatterman F (2005) Effects of parameter uncertainties on the  
826 modeling of terrestrial biosphere dynamics. *Global Biogeochemical Cycles*, **19**, GB3020.
- 827 Zhang F, Chen JM, Pan Y, Birdsey R.A., Shen S, Ju W, He L (2012) Attributing carbon  
828 changes in conterminous U.S. forests to disturbance and non-disturbance factors from 1901 to  
829 2010. *Journal of Geophysical Research: Biogeosciences*, **117**, G02021.