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

Running head: Biotic disturbance impacts across US forests

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Abstract

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

INTRODUCTION

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

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

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

Despite the undoubted relevance of BDs for shaping global forest ecosystems and influencing vegetation-climate feedbacks, impact assessments remain scarce at the larger spatial scale, i.e., beyond the local-to-regional context, and mainly focused on single agent-host systems. Process-based ecosystem models such as Dynamic Global Vegetation Models (DGVMs) are prime tools for investigating feedbacks between climate, vegetation, and disturbances over time and for quantifying terrestrial C cycle dynamics (Fisher *et al.*, 2014); however, incorporating BDs into these models is challenging due to the diversity and complexity of processes involved. Though the need for their incorporation has been repeatedly claimed for almost two decades now (Malmström & Raffa, 2000; Running, 2008; Arneth & Niinemets, 2010; Quillet *et al.*, 2010), BDs are typically very generically represented in current-generation DGVMs, e.g., as part of a spatio-temporally constant `background´ disturbance mortality rate integrating over several mortality processes that are not explicitly implemented elsewhere in the model (Kautz *et al.*, 2017). In cases where DGVMs have been extended towards a more explicit simulation of BD dynamics and impacts (e.g., Edburg *et al.*, 2011; Jönsson *et al.*, 2012; Medvigy *et al.*, 2012; Landry *et al.*, 2016), approaches (*i*) have focused on a single disturbance agent-host system only (one agent species affecting one host plant functional type, PFT), (*ii*) were restricted to insects (excluding pathogens and other BDs) and (*iii*) were limited in their spatial coverage (landscape to regional scales). Forest Landscape Models (FLMs), though typically operating at much finer spatio-temporal scales and process resolution than DGVMs, have also been applied to simulate ecosystem impacts at the landscape scale due to insects, pathogens and/or wildlife herbivory (e.g., Temperli *et al.*, 2015; Loehman *et al.*, 2017; Seidl & Rammer, 2017; De Jager *et al.*, 2017). For details on how BDs were considered in previous modelling approaches we refer the reader to S1 in the Supplementary Information where an overview is provided. To date, neither DGVMs nor FLMs has been applied at continental scales or larger, and considered multiple agent-host systems, thus limiting comparisons among different BD agents and regions.

This study aims to overcome these limitations by presenting a modelling approach that incorporates prescribed, spatio-temporally explicit disturbance fractions into a DGVM. By extending the model framework and applying comprehensive empirical disturbance data BD-induced impacts on forest C dynamics are simulated. In particular, we focus on quantifying the vegetation C loss, which is the amount of C that is transferred from living tree biomass to dead organic matter pools, as a consequence of BD-induced tree mortality and defoliation, and on assessing the relative importance of the different biotic agents on C cycling across US forests from 1997 to 2015.

MATERIAL & METHODS

Biotic disturbance data

The US Insect and Disease Survey database (IDS, USDA Forest Service, 2017), as used in this study, contains aerial-surveyed, annual and spatially explicit information of BD-induced forest disturbance across the 48 lower states and Alaska over the years 1997-2015. This data set is globally unique in respect to its extensive coverage and long-term consistency, combined with a high spatial, temporal, and attributive resolution (Kautz *et al.*, 2017). It consists of a freely accessible ArcGIS geodatabase containing approximately 3 million attributed BD polygons. Non-BD polygons in the IDS, e.g., abiotic disturbances, were excluded for this study. Disturbance polygons have been manually sketch-mapped during annual survey flights covering most of the US forests (Johnson & Wittwer, 2008). Each polygon is accompanied with several attributes, e.g., the BD type (tree mortality, defoliation, discoloration, topkill, among others), the causal BD agent and the affected host tree (both mainly given at species level). Further attributes characterizing damage severity and pattern would also provide valuable information, yet they have been inconsistently recorded over the spatio-temporal domain of the study and have thus not been included in the analysis herein. The rapid, subjective process of in-flight polygon delineation and attribution limits detection accuracy, and thus data may involve a certain level of generalization and inherent uncertainty (e.g., discussed in Meddens *et al.*, 2012; Kautz *et al.*, 2017). For instance, areas assigned as affected encompass healthy trees amongst damaged ones, which must be accounted for when reporting actual disturbed area (Meddens *et al.*, 2012). It should be also noted, that different polygons may spatially overlap within-year and between years. Both limitations were considered in the data processing described below. For details on standards of data acquisition and provision we refer the reader to the IDS documentation with updated Appendices E and F (USDA Forest Service, 2005).

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

Forest cover information for the study domain was obtained from the GLC2000 data set – a satellite-based global land cover classification for the year 2000 (Bartolomé & Belward, 2005), with vegetation classes 1 to 10 considered as forest in our analysis. We then created a 0.5° × 0.5° grid layer that was consistent with the model resolution, and intersected this grid with the disturbance data and the forest cover data. To account for within-year overlapping of polygons of similar BD types or agents we merged such polygons in a grid cell. Finally, we calculated the disturbance fraction D_f (%, =disturbed area / forest area × 100) for each grid cell and year separately for the selected BD types and agent groups. As an example, a grid cell might have been disturbed in a certain year by more than one type and/or agent, e.g., with $D_{f\ [\text{bark beetles}]}$=3%, $D_{f\ [\text{defoliators}]}$=1% and $D_{f\ [\text{pathogens}]}$=1.5% for tree mortality, and $D_{f\ [\text{defoliators}]}$=2.2%, $D_{f\ [\text{other insects}]}$=1.7% and $D_{f\ [\text{pathogens}]}$=1.2% for defoliation, giving a total disturbed fraction of 10.6%, of which 5.5% was mortality and 5.1% was defoliation.

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

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

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

[1] Insect and pathogen species were listed by genus names most representative for the agent group, but note that in exceptional cases species from one genus may belong to multiple agent groups.

[2] This category partially involves insects and/or pathogens.

LPJ-GUESS model

In this study we used a DGVM with an advanced representation of forest stand dynamics, the Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS). The model simulates vegetation dynamics, including demography, in response to varying environmental conditions and feedbacks between vegetation and soil (Smith *et al.*, 2001, 2014). Forest vegetation is represented by different PFTs (9 tree and two grass PFTs in this study), which are further distinguished in age cohorts. Stochastic processes associated with representation of growth and mortality are accounted for by the simulation (and averaging) of several replicate patches (20 in this study) for each of the 0.5° × 0.5° grid cells. Fire disturbances are modelled prognostically based on temperature, fuel load and moisture (Thonicke *et al.*, 2001), while stand-clearing \`background´ disturbances affect each patch randomly by a generic fraction of 0.01 yr^{-1} (Smith *et al.*, 2014); these baseline settings for non-biotic disturbances were not changed for this study.

Following a spin-up period of 500 years, the model was forced by gridded input considering variant land use patterns (LUH2; Hurtt *et al.*, 2016, as applied in Bayer *et al.*, 2017), and CRUNCEP climate, CO_2 concentration, and N deposition that were identical to simulations used in the global carbon project (Le Quéré *et al.*, 2016). Specifically for this study, a gridded annual BD fraction map (0.5° × 0.5°, described above) was applied for the period 1997-2015 in addition to other forcing, in order to prescribe fractions of tree mortality and defoliation caused by biotic agents.

Disturbance extension

We developed an extension to the current model framework, which improves the representation of stochastic disturbance events, e.g., due to biotic agents as presented in this study, or due to abiotic stressors like fire, storm, frost and drought. The extension allows for applying annually-prescribed disturbance fractions regarding two principal disturbance types, tree mortality and defoliation, for any given time period or region across the globe and irrespective of the causal agent or stressor. Though the extension is principally applicable also to abiotic disturbances in this study it was only applied for BDs.

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

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

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

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

Simulations and analyses

In a first step, we established a gridded map based on the IDS data and identified tree mortality and defoliation patterns caused by different BD agents across US forests. These gridded maps were then applied as fractional disturbances in LPJ-GUESS to simulate BD-induced C fluxes from live to dead biomass pools, separated by BD types and agents. Simulations were carried out for all BD-affected grid cells that were covered by climate data and land use data, resulting in a total of 2009 grid cells with prescribed tree mortality and 1663 grid cells with prescribed defoliation. We also ran the model with a homogeneous BD fraction, i.e., a mean D'_f applied over all affected grid cells and years, which allowed assessing the effect of spatio-temporal variability in BD occurrence.

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

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

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

RESULTS

Disturbance pattern

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

There were distinct spatial hotspots for both disturbance types with highest mortality fractions occurring in the mid-western states (Colorado, Wyoming) and notable defoliation in the north-eastern US (Minnesota, Wisconsin). Temporal trends for both types did not indicate any increase or decrease over the study period, yet disturbance magnitude strongly varied between years, mainly as a consequence of ephemeral insect and pathogen outbreaks (Fig. 1 insets). The contribution of different agents varied among BD types, and across space and time (Fig. 2): overall, bark beetles were responsible for most tree mortality and defoliator insects were the dominant agents causing defoliation, i.e., 72% and 89% of the totals, respectively. Host types were not equally affected by mortality and defoliation: while (non-lethal) defoliation disturbed mainly broadleaf trees (51%, with 24% conifers and 25% mixed/unknown), mortality predominantly befell conifers (77%, with 5% broadleaf and 18%, mixed/unknown). In the western US and Alaska, tree mortality was principally caused by bark beetles, e.g., outbreaks of mountain pine beetle and spruce beetle, with smaller contribution from pathogens, e.g., causing sudden oak death in California, and other biotic agents. In the eastern US, all five agent groups contributed more equally to tree mortality, including defoliators, e.g., eastern spruce budworm, forest tent caterpillar and gypsy moth, and other insects, e.g., hemlock and balsam woolly adelgid. In contrast, defoliation –often a trigger of subsequent tree mortality– was dominantly caused by defoliators across the entire study domain and to much lesser extent also by other insects and pathogens.

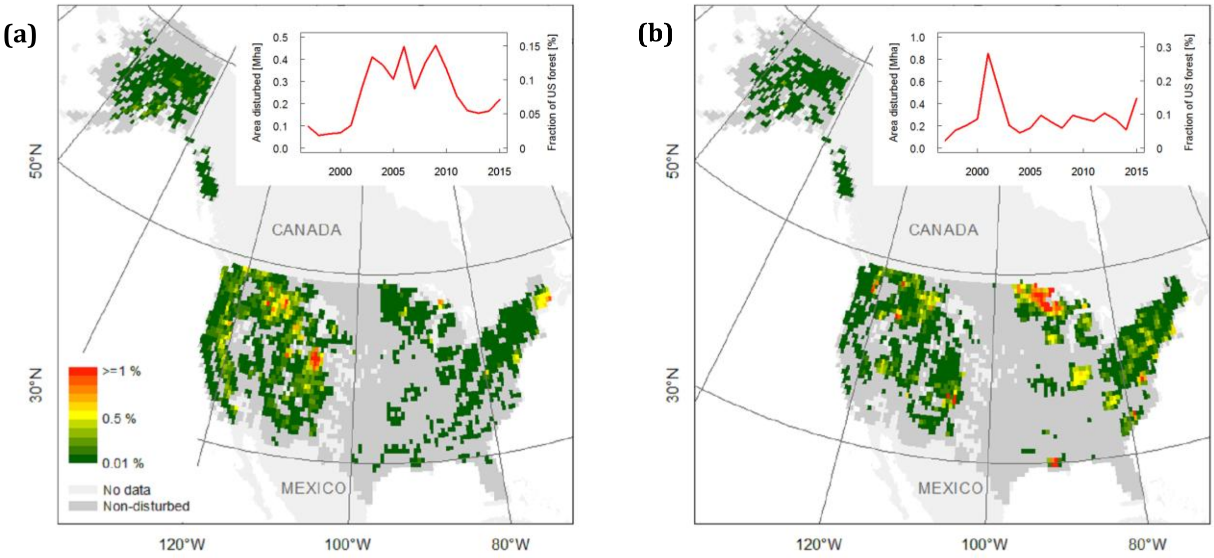

Figure 1. *Biotic disturbance-induced tree mortality (**a**) and defoliation (**b**) across US forests in 1997-2015. Maps show mean annual disturbance fraction* D'_f *(% of forest area) in each grid cell as used for simulations; no data = grid cells not covered by forest, climate or land use forcing,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

Disturbance-induced C fluxes

The total amount of C transferred from live to dead biomass pools due to BD over the study period summed up to 251.6 Mt C, or an annual mean of 13.2 Mt C yr^{-1} (SD: ±7.3 Mt C yr^{-1} between years; Table 2). C fluxes from BD-induced tree mortality were approximately twentyfold higher compared to defoliation with a total of 239.5 Mt C (12.6 ±7.3 Mt C yr^{-1}) and 12.1 Mt C (0.6 ±0.4 Mt C yr^{-1}), respectively. Overall, bark beetles impacted the forest C cycle most (60.6% of total flux), followed by other insects (14.9%), other biotic agents (13.6%), defoliator insects (6.0%) and pathogens (4.9%). That means insect-associated impacts were about five times higher than non-insect agents. Both spatial and temporal C flux patterns broadly followed those of BD occurrence, exhibiting a notable variability among grid cells and years, yet without indicating a clear temporal trend (Fig. 3). Highest impacts with fluxes >100 kg C ha^{-1} yr^{-1} occurred in the states of California, Colorado, Washington, Oregon, Idaho, Montana, Wyoming and Maine, where moderate-to-high mortality fractions coincide with high simulated tree biomass C density (Fig. 1, 3 and 5). Similar to the BD occurrence, agent contribution to total fluxes varied among BD types, and across space and time (Fig. 2): while bark beetles dominated mortality C fluxes in the western states and Alaska with a more mixed contribution of all groups in the eastern states, defoliator insects most contributed to defoliation C fluxes over large parts of the US forests.

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

Table 2. *Biotic disturbance-induced carbon flux from live to dead biomass pools for US 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

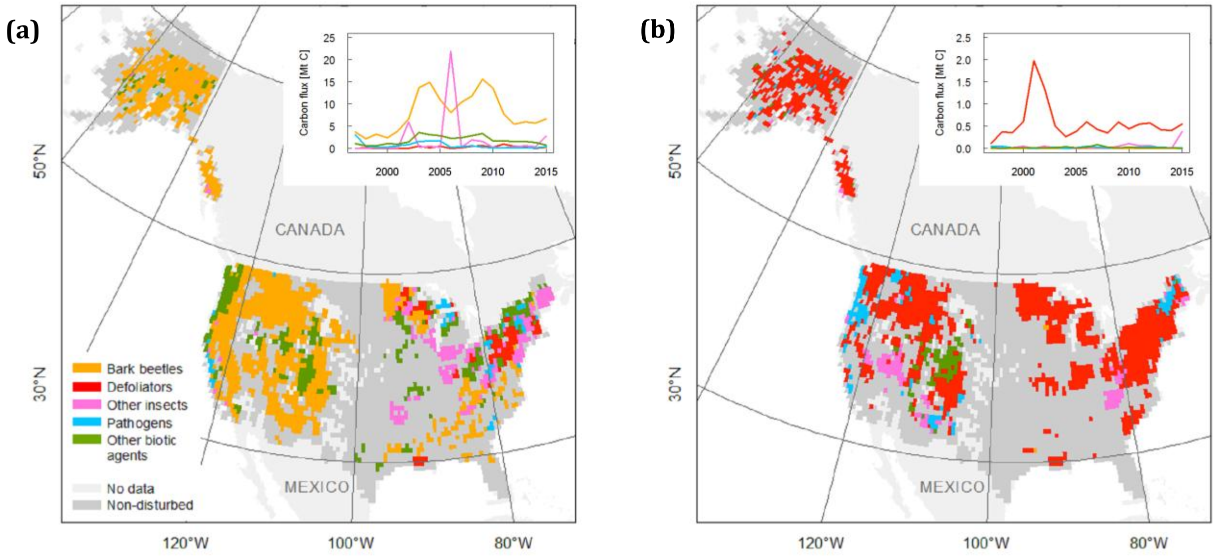

Figure 2. *Biotic disturbance agent contribution to tree mortality (**a**) and defoliation (**b**) across US forests in 1997-2015. Maps show the dominant agent in each grid cell concerning both mean disturbance fractions and associated mean carbon fluxes; no data = same as in Fig. 1. Insets indicate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

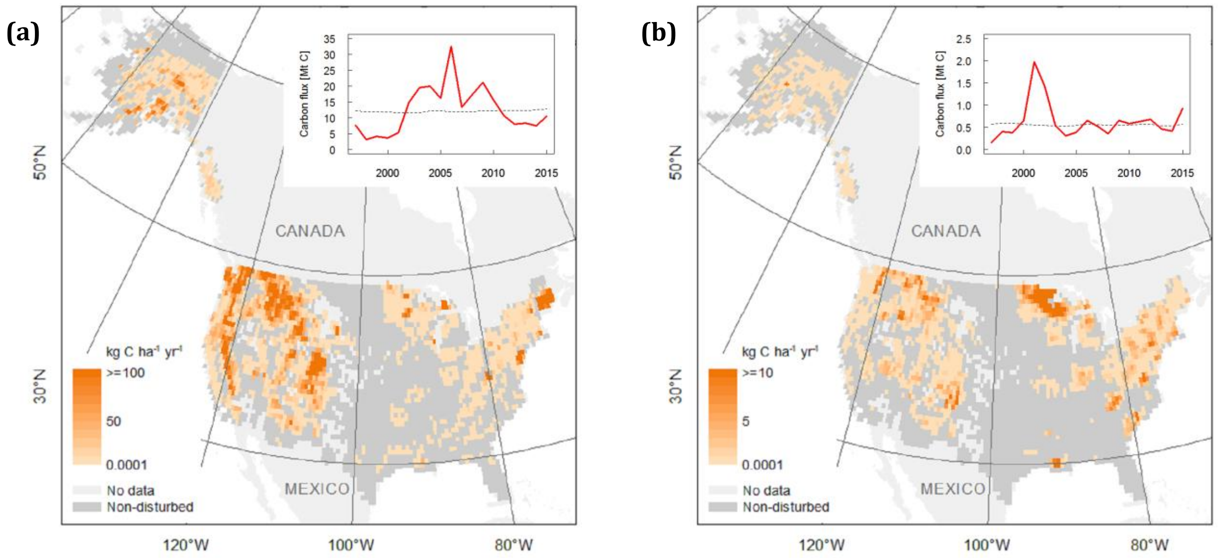

Figure 3. *Biotic disturbance-induced carbon fluxes from live to dead biomass pools through tree mortality (**a**) and defoliation (**b**) across US forests in 1997-2015. Maps show simulated mean annual carbon fluxes (kg C ha^{-1} yr^{-1}) in each grid cell; no data = same as in Fig. 1. Insets indicate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

Uncertainty in simulated C fluxes

Simulated C fluxes through BD-induced tree mortality and defoliation were notably affected by both tested parameters, the correction factor *CF* and the tree age threshold *TA* (Fig. 4). An increased *CF* resulted in linearly increased C fluxes, a pattern that is mostly independent from *TA* and that is explained by the direct determination of the disturbance fraction D'_f through *CF* (Fig. 4a,b). In contrast, tree age was less influential for simulated C fluxes and the effect was not consistent over the entire range of tested *TA*-values: while fluxes increased with tree age until *TA*≤10, they decreased with increasing tree age for *TA*≥10 (Fig. 4c,d). Such negative correlation of *TA* and C fluxes is counter-intuitive since vegetation C pools typically increase with tree age, yet it can be explained by the reduced availability of older susceptible trees to be disturbed in a grid cell. As a result, in grid cells with insufficient older trees simulated disturbance fractions were lower than originally prescribed, thus leading to a potential underestimation of C fluxes at higher *TA* and in particular under high *CF* scenarios. Nevertheless, our default scenario *CF*=0.1 was only slightly affected by modified *TA*: the chosen default value of *TA*=20 provided C fluxes that are robust compared to the entire range of *TA* values tested (red lines in Fig. 4c and d). Overall, our sensitivity experiments suggest that the presented results based on default settings *CF*=0.1 and *TA*=20 provided rather conservative estimates regarding the range of potential C fluxes of 1.9-36.1 Mt C yr^{-1} for tree mortality (Fig. 4a,c) and 0.1-2.1 Mt C yr^{-1} for defoliation (Fig. 4 b,d). The *CF* and *TA* parameter dependent uncertainty for total BD-induced C fluxes ranged from 38.0 to 725.8 Mt C, i.e., 2.0-38.2 Mt C yr^{-1}.

Evaluation of simulated vegetation C density

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

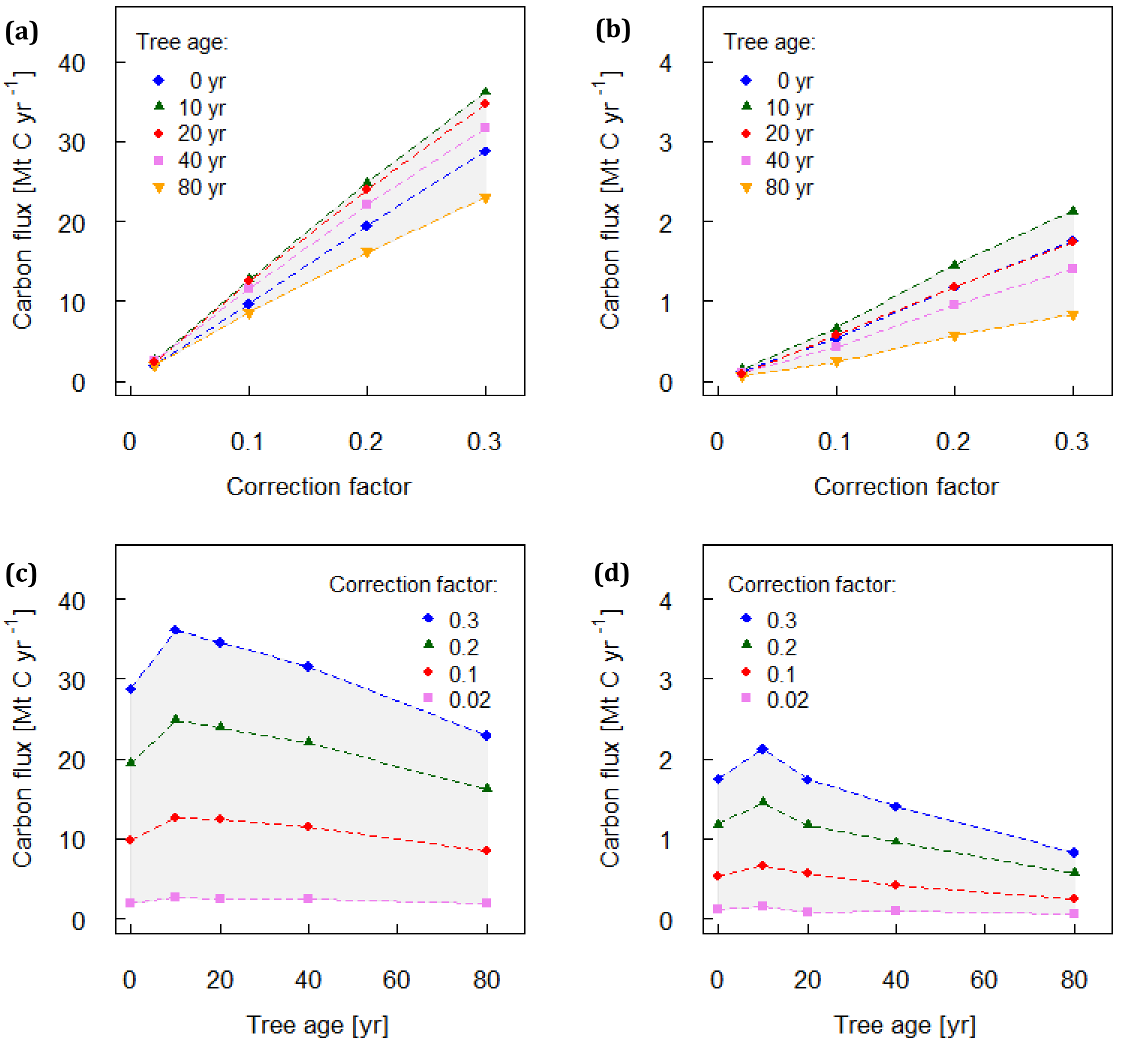

Figure 4. *Effect of varying model parameters on biotic disturbance-induced carbon flux from live to dead biomass pools through tree mortality (**a**, **c**) and defoliation (**b**, **d**). Given are mean annual carbon fluxes (Mt C yr^{-1}) for the period 1997-2015, summed over all disturbed grid cells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

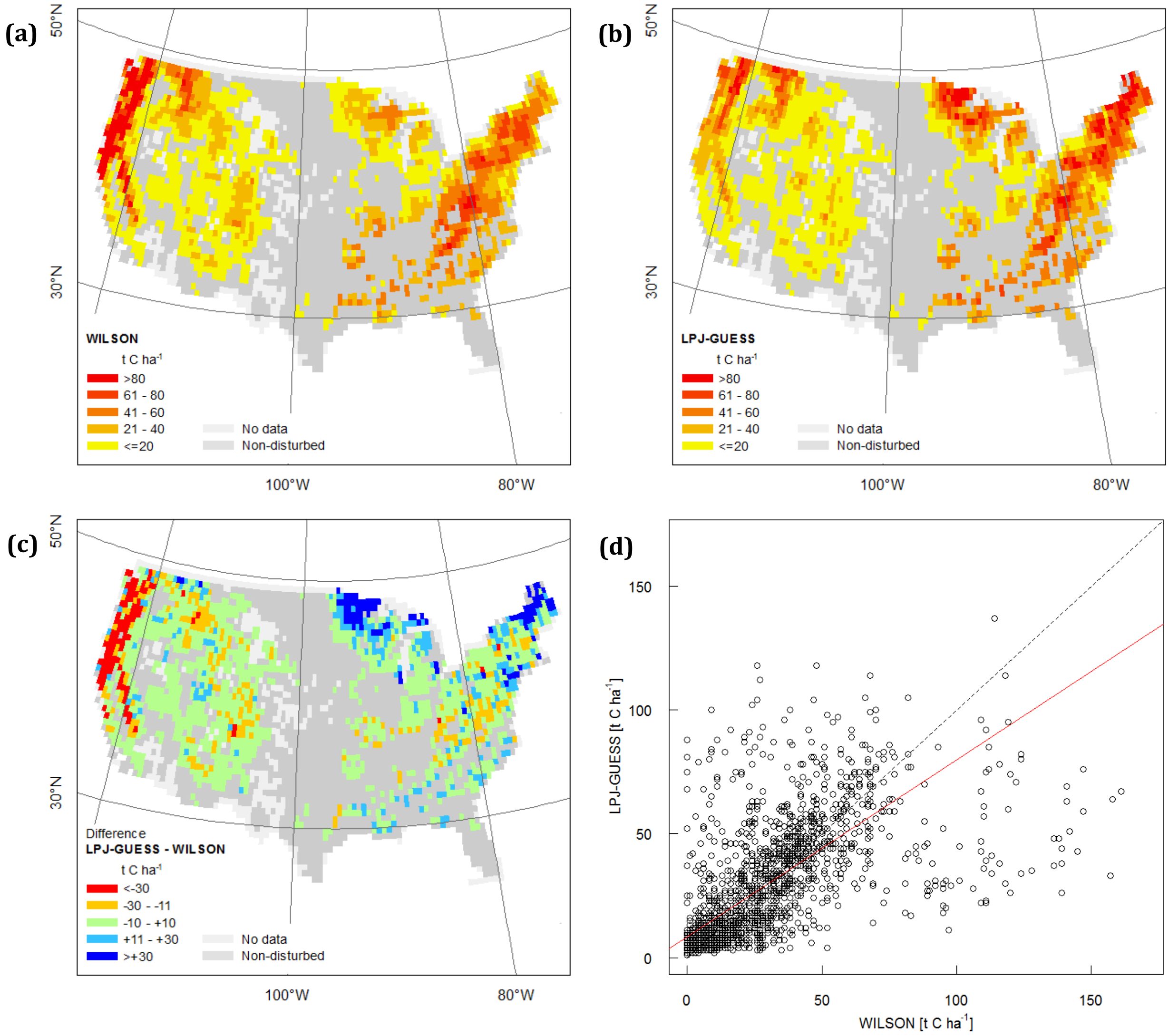

Figure 5. *Forest vegetation carbon density (mean of years 2000-2009) in grid cells affected by biotic disturbances across the conterminous US during the study period 1997-2015 (n=1645):* ***a)*** *observations according to Wilson et al. (2013),* ***b)*** *LPJ-GUESS model output,* ***c)*** *difference,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

DISCUSSION

By providing the first continental-scale DGVM-based assessment of BD-induced impacts on forest C cycling, i.e., vegetation C loss, this study contributes to improve our quantitative understanding beyond the regional scale and single agent-host systems. In particular it allows for comparisons across regions, BD types and agents. The pronounced C flux variability over space and time emphasizes the relevance of considering spatio-temporal variability of disturbances in ecosystem models in order to better explain observed C cycling patterns. Such consideration will also be important to disentangle the contribution from different disturbances, e.g., BDs, fire and harvesting, as well as non-disturbance factors, e.g., CO_2, N deposition and climate (Zhang *et al.*, 2012; Le Quéré *et al.*, 2016; Williams *et al.*, 2016). Yet, this finding further calls for intensified forest monitoring efforts to provide BD data at an adequate resolution, e.g., annually and at sub-national level. To date, accurate assessments of BD impacts on C cycling are largely impeded by the limited availability and resolution of such data regarding most of the global forests (Kautz *et al.*, 2017).

According to our simulations BD-induced tree mortality and defoliation reduced annual GPP in forests by an average 21.6 Mt C yr^{-1} (0.4% of total), and annual NPP by 5.8 Mt C yr^{-1} (0.3%), when compared to simulations excluding BDs. Likewise, average BD contribution to total vegetation C turnover time was relatively low, i.e., approximately 3% of the total tree mortality-caused C flux was due to BDs, and the good performance of LPJ-GUESS in simulating forest biomass (Fig. 5) gives confidence in the broad magnitude of this outcome. A similar contribution to turnover has been estimated for the period 1990-2008 in managed Canadian forests (Stinson *et al*., 2011). These figures indicate a rather marginal effect of BDs on C dynamics and forest productivity at the larger spatio-temporal scales, which can be explained by the low average disturbance fraction (e.g., 0.08% annual mean tree mortality across our study domain). In contrast, substantial ecosystem response has been shown to occur above a disturbance fraction threshold of approximately 40-60% (Flower & Gonzales-Meler, 2015; Stuart-Haëntjens *et al.*, 2015), as typically reported for outbreaks temporally affecting the plot- to landscape scale (e.g., Pfeifer *et al.*, 2011; Hicke *et al.*, 2012; Bright *et al.*, 2013; Flower *et al.*, 2013). For instance, NPP was reduced by 31% due to emerald ash borer-caused tree mortality across 45 sample plots over a 7-year period in Ohio (Flower *et al.*, 2013), and aboveground tree C stocks were reduced by 40-50% in a severely bark beetle-disturbed landscape over a 8-year period in Idaho (Bright *et al.*, 2013; see also Hicke *et al.*, 2012 for additional examples).

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

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

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

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

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

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

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

Despite given differences in model parametrization and structure the presented approach may serve as a blueprint for other DGVMs or similar models with potential for further development and adaption, e.g., regarding (*i*) the variation of BD-related parameters *CF* and *TA* according to the agent-host systems investigated, (*ii*) additional host specifying factors, such as considering single species or temporal drought stress, (*iii*) the implementation of snag dynamics that account for delayed C and N fluxes, and (*iv*) the capacity of the tree to reflush within-season following defoliation. Future disturbance trajectories can be simulated by modifying disturbance fractions, e.g., altered fractions or shifted ranges as projected for some bark beetles in the US as a consequence of climate warming (Bentz *et al.*, 2010). Ultimately, however, process-based representation of BDs – though it is challenging – needs to be refined in the next-generation of DGVMs, thereby enabling the simulation of dynamic feedbacks between CO_2, climate, vegetation and disturbances, as well as of interactions between different disturbances, and interactions between disturbances and forest management.

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SUPPLEMENTARY INFORMATION

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

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