2015

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Repository Citation

Ghimire, Bardan; Williams, Christopher A.; Collatz, G. James; Vanderhoof, Melanie; Rogan, John; Kulakowski, Dominik; and Masek, Jeffrey G., "Large carbon release legacy from bark beetle outbreaks across Western United States" (2015). *Geography*. 286.
https://commons.clarku.edu/faculty_geography/286

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Received Date : 07-Jun-2013
Accepted Date : 31-Jan-2015
Article type : Primary Research Articles

Large Carbon Release Legacy from Bark Beetle Outbreaks across Western United States

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Keywords: Carbon cycle, bark beetle, disturbances, forests, biogeochemistry.

Paper type: Primary Research Article

Abstract

Warmer conditions over the past two decades have contributed to rapid expansion of bark beetle outbreaks killing millions of trees over a large fraction of western United States (US) forests. These outbreaks reduce plant productivity by killing trees, and transfer carbon from live to dead pools where carbon is slowly emitted to the atmosphere via heterotrophic respiration which subsequently feeds back to climate change. Recent studies have begun to examine the local impacts of bark beetle outbreaks in individual stands but the full regional carbon consequences remain undocumented for the western US. In this study, we quantify the regional carbon impacts of the bark beetle outbreaks taking place in western US forests. The work relies on a combination of post-disturbance forest regrowth trajectories derived from forest inventory data and a process-based carbon cycle model tracking decomposition, as well as aerial detection survey (ADS) data documenting the regional extent and severity of recent outbreaks. We find that biomass killed by bark beetle attacks across beetle affected areas in western US forests from 2000 - 2009 ranges from 5 to 15 Tg C yr^{-1}, and caused a reduction of net ecosystem productivity (NEP) of about 6.1 to 9.3 Tg C y^{-1} by 2009. Uncertainties result largely from a lack of detailed surveys of the extent and severity of outbreaks, calling out a need for improved characterization across western US forests. The carbon flux legacy of 2000-2009 outbreaks will continue decades into the future (e.g. 2040-2060) as committed emissions from heterotrophic respiration of beetle-killed biomass are balanced by forest regrowth and accumulation.

Introduction

Bark beetle infestations have been increasing in recent decades across western United States (US) forests with millions of hectares affected (Dale *et al.*, 2001, Raffa *et al.*, 2008). The predicted regional increase in temperatures associated with climate change are likely to lead to further rises in bark beetle outbreaks (given that there are enough host trees available) caused by accelerating bark beetle life cycles resulting in faster reproduction, and also weakening of host trees by heat and drought stresses (Logan *et al.*, 2003, Raffa *et al.*, 2008). Bark beetle outbreaks are likely to occur in new locations as bark beetle populations move further northwards and to higher elevations as temperatures rise (Bentz *et al.*, 2010, Carroll *et al.*, 2004, Hicke *et al.*, 2006, Williams & Liebhold, 2002). Regions that previously had small bark beetle populations are affected by more severe outbreaks (Raffa *et al.*, 2008). Bark beetle outbreaks could also increase in southern and lower elevation regions, if sufficient host trees are available but these regions that historically experienced high disturbance rates could have reductions in infestations related to decreases in host trees associated with past disturbances, such as, harvest, insects and fires, and also as higher temperatures create adverse conditions that are less suitable for bark beetle eruptions (Carroll *et al.*, 2004, Logan & Bentz, 1999).

Bark beetle outbreaks usually occur within the range of their host species (e.g. Douglas-fir, mountain pine and spruce beetles target Douglas-fir, pine and spruce forests respectively) and reproduce in the inner phloem tissue of trees (Amman *et al.*, 1977, Bebi *et al.*, 2003, Kulakowski *et al.*, 2003, Schmid & Frye, 1976, Weatherby & Thier, 1993). At the initiation of the outbreak, bark beetles usually infest old (mature) trees of large diameter which have been weakened by fires, high temperature stress, drought, disease and/or physical damage (Raffa *et al.*, 2008). Trees counter the bark beetle attacks by producing resin that can injure bark beetles (Raffa *et al.*, 2008). However, as the population of bark beetles increases the beetles overwhelm the tree defenses, and during large and severe outbreaks even smaller diameter host trees become susceptible to infestation (Aukema *et al.*, 2006, Raffa *et al.*, 2008). The visual symptoms of mortality caused by bark beetle infestation can unfold over multiple years with needles initially turning red (red stage), and then dropping and accumulating as litter on the forest floor, leaving the gray limbs/branches (gray stage).

Bark beetle infestations have both physical and biological effects leading to substantial changes to forest ecosystems (Samman & Logan, 2000). Bark beetle outbreaks cause tree mortality leading to changes in forest structure and composition (Bigler *et al.*, 2005, Jenkins *et al.*, 2008). Beetle-killed forests are characterized by a higher proportion of standing dead trees (snags), and have more coarse woody debris and fine litter than before disturbance (Jenkins *et al.*, 2008, Jorgensen & Jenkins, 2011, Klutsch *et al.*, 2009). This can lead to elevated resource availability for surviving trees due to increased light, nutrients and moisture at the forest floor (Stone & Wolfe, 1996). Modifications in the biotic and abiotic environment can alter future disturbance regimes, and lead to transformations in size, distribution and composition of forests (Collins *et al.*, 2011, Simard *et al.*, 2011). These structural and compositional changes impact forest function including water (Hélie *et al.*, 2005), energy (Amiro *et al.*, 2006), and carbon (Edburg *et al.*, 2011, Kurz *et al.*, 2008, Stinson *et al.*, 2011) balances.

The primary mechanism of bark beetle impacts to ecosystem carbon balance is through foliage loss and tree mortality, and the associated reduction in productivity (Hicke *et al.*, 2012). However, a few years after the insect infestation, forests regenerate and can attain or exceed pre-disturbance productivity levels depending on nutrient status, seed and sapling availability, climatic conditions, and competition. Bark beetle infestation also results in the accumulation of beetle-killed biomass on the forest floor (Hicke *et al.*, 2012). Microorganisms, such as bacteria and fungi, decompose the newly available litter and woody debris, with rates controlled by climatic conditions (e.g., temperature and moisture availability) and substrate quality (Fierer *et al.*, 2005, Harmon *et al.*, 1986, Kätterer *et al.*, 1998, Schlesinger & Andrews, 2000). The decomposition of beetle-killed biomass releases carbon to the atmosphere via heterotrophic respiration (Hicke *et al.*, 2012, Kurz *et al.*, 2008).

The few studies that have analyzed the carbon consequences of bark beetle outbreaks have reported a range of impacts on carbon budgets. Large area studies conducted in the Montane Cordillera zone in Canada have reported huge beetle impacts on the carbon balance with indirect carbon emissions equivalent to approximately 75% of the average direct Canadian fire emissions, and average transfer of 25 Tg C yr^{-1} from live biomass pools to dead pools (Kurz *et al.*, 2008, Stinson *et al.*, 2011). Recent work by Hicke *et al.* (2013) using methods different from those reported here (i.e., by overlaying maps of forest mortality and carbon stocks) indicated that the carbon in bark beetle killed trees in western US amounts to 1.8 – 24.4 Tg C yr^{-1} with a realistic middle estimate of 20.6 Tg C yr^{-1} which is less than that reported by Kurz *et al.* (2008) for the outbreak in British Columbia. Forest recovery rates and associated carbon accumulation following bark beetle outbreaks depend on the damage severity of the outbreak and spatial scale of the study. Landscape scale studies estimate that carbon sources persist for multiple decades following severe beetle outbreaks (Kurz *et al.*, 2008). In contrast, small scale studies conducted at plot scales show that stands are carbon sources in the early years (Brown *et al.*, 2010), and usually recover to pre-disturbance levels between 10 to 25 years (Pfeifer *et al.*, 2011, Romme *et al.*, 1986). This recovery is attributed to the increased productivity and growth of remaining trees and understory vegetation (Brown *et al.*, 2010). This discrepancy in post-disturbance recovery time occurs between large and small scale studies partly because large scale studies consider the dynamic nature of bark beetle disturbances (with some forest areas recovering from disturbances while other forest areas recently affected by disturbances) across large areas in multiple years with mosaic of differing forest ages where most of the severe disturbances have occurred recently converting these forests into carbon sources whereas small scale studies that use field-based observations capture finer scale processes caused by a single bark beetle event over a given time period. Other likely explanations for the discrepancy include differences in the severity (i.e., biomass killed) of bark beetle disturbances analyzed (e.g., high severity versus low severity) as well as differences in methodology (e.g., aerial surveys and modeled flux trajectories versus fluxes derived from field-based measurements) (Moore *et al.*, 2013).

Most of these prior studies have had limited temporal and/or spatial extents, analyzed only a subset of bark beetle types, or focused in the Canadian Montane Cordillera zone. None have examined the impact of multiple beetle types on ecosystem productivity and post-disturbance recovery across the entire bark beetle infested forest area in the western United States. This study assesses the impact of major bark beetle types on carbon stocks and fluxes in forests of the western United States. The specific questions addressed by this study are: 1) How do bark beetle affected area, biomass and mortality differ by forest types, and regions? 2) What are the historical and legacy consequences of bark beetle damage for forest carbon stocks and fluxes across the region?

Materials and methods

The approach in this study involves two key pieces of information, namely 1) forest carbon fluxes following beetle outbreaks of varying severity and in different forest types and regions, and 2) the areal extent and timing of beetle outbreaks. For the first we develop characteristic post-disturbance carbon flux trajectories by expanding the approach of Williams et al. (2012) to account for the specific effects of bark beetle induced mortality on carbon balance. For the second we rely on the United States Forest Service (USFS) Aerial Detection Survey (ADS) dataset that characterizes the area of outbreaks in recent years and records the corresponding mortality of trees. Procedures for determining each of the two key pieces of information are described in the next sections. The modeling approach involves running the model for a single point (from spin-up to an imposed bark beetle disturbance and tracking the legacy effects) for each unique combination of six forest types, four regions, two site productivity classes and 1680 severity (i.e., disturbance-killed) levels because a long record of biomass chronosequences are available from the forest inventory data for these unique combinations to constrain our model. This type of approach to derive post-disturbance trajectories by disaggregating different heterogeneous land units is conceptually similar to approaches used by Zhang *et al.* (2012), Kurz *et al.* (2008) and Williams *et al.* (2012). The model's productivity and decomposition rates depend on temperature and precipitation, which are prescribed with climatologies from the following data sets. Monthly air temperature anomalies at one degree are derived from Goddard Institute of Space Studies (GISS) (Hansen et al., 1999) dataset for 1982 to 2005 and subsequently added to temperature climatology (Leemans & Cramer, 1991). Monthly precipitation climatologies are obtained from the one degree Global Precipitation Climatology Project (GPCP) (Adler et al., 2003) dataset from 1982 to 2005. These temperature and precipitation fields are resampled using nearest neighbor to the resolution of the 0.002243 x 0.004912 degree forest map (Ruefenacht et al., 2008). Temperature and precipitation climatologies are extracted as spatially averaged values for combinations of forest types and forest service regions.

We further scale our carbon fluxes to a regional domain by applying the areal proportions of bark beetle disturbed areas in each unique combination of forest type, region, site productivity class and severity levels. Our analysis of carbon impacts focuses on bark beetle infested areas across the entire western United States forests and we do not consider forest areas affected by other disturbance types, such as harvest and fires. This area affected by current bark beetles in western US forests is unprecedented, and exceeds four million hectares (Man, 2010). Figure 1 shows the schematic of the methodology used in this study to integrate an ecosystem model with forest inventory and aerial survey data to estimate the regional carbon balance due to bark beetles outbreaks.

Derivation of characteristic post-disturbance carbon flux trajectories

The generation of characteristic post-disturbance carbon flux trajectories with stand age is primarily based on the method of Williams and others (2012). This method relies on the Carnegie-Ames-Stanford Approach (CASA) carbon cycle model run at a monthly time step to simulate net primary productivity (NPP) and heterotrophic respiration as a function of stand age for unique combinations of forest type, region, and site productivity class. CASA uses a light use efficiency based approach (driven in our case by remotely sensed 1 km spatial resolution fraction of photosynthetically active radiation MOD15A2 product (Nightingale *et al.*, 2009) sampled for each forest type group by region) to model NPP. In the present work, modeled NPP is further constrained by forest inventory data, whereby we adjust NPP for specific settings of forest type, region and productivity class such that modeled aboveground biomass accumulation with stand age matches that observed in forest inventories (see Williams *et al.*, 2012). We simulate biomass accumulation with stand age for a family of possible NPP and wood turnover rates and select the pair that best fits a chronosequence of aboveground biomass observed for forests of varied stand ages.

The CASA model simultaneously estimates heterotrophic respiration (Rh, meaning decomposition of dead carbon pools), and inter-pool carbon transfers (including those induced by disturbances) using a century model type decomposition cascade. The default turnover times for the parameters that control decomposition are 14.8 yr^{-1} for surface metabolic, 3.9 yr^{-1} for surface structural, 18.5 yr^{-1} for soil metabolic, 4.8 yr^{-1} for soil structural, 0.25 yr^{-1} for woody debris, 6 yr^{-1} for surface microbial, 7.3 yr^{-1} for soil microbial, 0.2 yr^{-1} for slow soil and 0.0045 yr^{-1} for armored soil pools. We further modified and sub-divided the default woody debris pool into a slow woody debris pool representing the dynamics of snags and downed dead wood and a fast woody debris pool representing the dynamics of fine woody debris. The slow woody pool has a turnover time of 0.01 yr^{-1} (i.e., residence time of 100 years) and is consistent with field- based observations of the decomposition dynamics of snag and downed coarse dead wood occurring over decades to centuries (Harmon *et al.*, 1986, Moore *et al.*, 2013), and the fine woody debris pool has a turnover time of 0.1 yr^{-1} (i.e., residence time of 10 years) (Fasth *et al.*, 2011).

Net ecosystem productivity (NEP) is then computed as the difference of net primary productivity and heterotrophic respiration. We start with an initial spin-up of the CASA model using the selected NPP and wood turnover parameters to achieve a steady-state condition for live and dead carbon pools and associated fluxes. We then impose an initial stand-replacing harvest disturbance to simulate the secondary forest condition typical of nearly all US forests today. The harvest disturbance involves killing trees and transferring some of the carbon to dead pools while taking a portion off site. The fraction taken off site is informed by knowledge of harvesting practices and also constrained by the biomass chronosequences. Carbon pools are then allowed to refill to the average stand age for particular forest type groups according to forest inventory and analysis (FIA) data. Aboveground biomass chronosequences are obtained from the inventory data by dividing live aboveground biomass by the area sampled for unique combinations of forest types, productivity levels and forest service regions. Four forest service regions in the western United States are considered, namely Pacific Northwest (PNW), Pacific Southwest (PSW), Rocky Mountain North (RMN) and Rocky Mountain South (RMS). The six forest types considered in this study are Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*) and whitebark pine (*Pinus albicaulis*). The two productivity levels utilized are based on categorizing the productivity values reported by FIA into high (120 to >225 cubic feet acre^{-1} annum^{-1}) and low (20 to 119 cubic feet acre^{-1} annum^{-1}) productivity classes. Additional details of the general modeling procedure up to this point are described in Williams *et al.* (2012).

Unlike in our prior work, in this paper the final stage of the model exercise imposes an insect-induced partial disturbance resulting in partial vegetation mortality. This involves transferring a certain percentage (<100%) of the live carbon pools to dead pools, and allowing live pools to regrow. This final modeled series provides the characteristic carbon flux trajectories over time for different forest types, regions, productivity classes, and beetle attack severity levels (i.e., bins for biomass killed per area by bark beetles). Additionally, the pre-disturbance trajectory is tracked beyond the average age of forest type groups to provide a control scenario representing the potential trajectory in the absence of beetle infestation. In the bark beetle affected areas, the differences in the trajectory in the absence of bark beetle infestation, and the trajectory generated by imposing the historical bark beetle infestation quantifies the reduction in productivity due to bark beetles. Further details are provided in the supporting information.

Quantifying recent beetle-induced mortality

The USFS ADS dataset reports severity as the number of trees affected by bark beetles per unit area. However, our trajectory-based carbon pool modeling approach does not simulate stand age structure or individuals but rather bulk live biomass in wood (above- and below-ground), leaves and fine roots. As a result, in our study bark beetle severity refers to the mortality due to bark beetles expressed as live biomass killed per area. Live biomass was used because it is widely available for US forests, and is also correlated to other structural variables, such as stand height, and leaf area. Therefore, we had to convert the number of trees affected by bark beetles per area to biomass affected by bark beetles per area using FIA data. The FIA database version 4, is queried for county-level biomass and number of trees for Douglas-fir, Engelmann spruce, lodgepole pine, ponderosa pine, whitebark pine, and western white pine forest types based on age or diameter classes having high susceptibility for bark beetle attack. Forest types are attacked by specific bark beetle types. For example, Douglas-fir forests are attacked by Douglas-fir beetle (*Dendroctonus pseudotsugae*), Engelmann spruce forests by spruce beetle (*Dendroctonus rufipennis*), and lodgepole pine, ponderosa pine, whitebark pine and western white pine forests by mountain pine beetle (*Dendroctonus ponderosae*). Douglas-fir beetles and mountain pine beetles (MPB) are assumed to attack stands with age older than 120 years (Weatherby & Thier,

1993) and 80 years (Amman *et al.*, 1977), respectively, and spruce beetles are assumed to prefer stands with diameter larger than 16 inches (Schmid & Frye, 1976). Subsequently, the ratio of total biomass to total number of trees is obtained from querying the FIA database for different forest types in each western United States County. Missing values for the county-specific ratio of total biomass per total trees are interpolated from the nearest county. The number of trees killed by bark beetle per area (N_{killed}, trees m^{-2}) reported by ADS data is multiplied with corresponding county-level FIA derived average live aboveground biomass per tree (B_{tree}, kg C tree^{-1}) based on age or diameter classes having high susceptibility for bark beetle attack in order to obtain biomass per area killed (B_{killed}, kg C m^{-2}) for each insect (bark beetle) outbreak polygon as:

$$B_{killed} = N_{killed} \times B_{tree} \tag{1}$$

The biomass per area killed is further binned into different bark beetle severity levels. Uncertainties due to the number of trees killed (as reported by ADS) are quantified in this study by providing two additional scenarios where biomass killed is multiplied by factors of 3 and 10 (upper limit), in addition to reporting the scenario without any biomass correction (lower limit). These biomass multipliers are also consistent with those reported in Meddens *et al.* (2012) as well as our own field-based analysis conducted at the Colorado's Front Range. Further details are provided in the supporting information.

Quantifying carbon consequences of recent outbreaks

Regional carbon fluxes are estimated for the ADS-mapped bark beetle outbreaks of recent decades by applying the characteristic carbon flux trajectories to areas of outbreak. The assessment involved two NEP estimates, a reference control estimate using the characteristic trajectory of NEP in the absence of disturbance, and a severity-specific NEP trajectory that includes effects of beetle infestation. The difference is used to represent the impact of the beetle disturbance in terms of NEP reduction. The reference control represents the background effect of an age structure legacy from past disturbance that would have persisted in the absence of bark beetle disturbance, also assuming that forests remain undisturbed by other factors. Further details are provided in the supporting information.

An additional measure of NEP reduction is also determined under the assumption that both bark beetle infested and control areas could further be disturbed by fire and harvest disturbances. As a result, two simulations are performed, a reference control with only fire and harvest disturbances and a case also with beetle outbreaks for 200 severity levels (i.e., bins for biomass killed per area by bark beetles). The simulations for the bark beetle scenario consists of applying stand replacing harvest or fire disturbances to trajectories recovering from different bark beetle disturbance severities. The control involves applying the same rate of stand replacing harvest or fire disturbances but to trajectories in which forests continually aged from the specified pre-beetle attack stand age. Stand replacing disturbances are probabilistically applied based on the percent of forest area affected by harvest and fires.

Harvest and fire rates for each region of the western US were determined from the most recent full report by the US Forest Service (Smith *et al.*, 2009), and the MTBS dataset (Eidenshink *et al.*, 2007), respectively. Annually harvested area is reported for timberlands only for the PNW, PSW, Intermountain regions, where Intermountain includes both RMS and RMN states. The RMS and RMN split was inferred based on their proportional contributions to total growing stock removals, yielding a 53.5% and 46.4% split for RMS and RMN regions.

Harvested areas were divided by the total area of timberland by region, yielding harvest rates of 1.26%, 1.40%, 0.69%, and 1.06% per year for the PNW, PSW, RMN, and RMS regions respectively. The rate of stand-replacing fire was estimated from the average annual area burned by high severity fire during 1999 to 2008 as reported in the MTBS dataset divided by the total forested area, calculated for each region separately. This yielded stand-replacing fire rates of 0.08%, 0.25%, 0.26%, and 0.07% per year for the PNW, PSW, RMN, and RMS regions respectively. The total area harvested and burned with high severity annually averaged 5478 km^2 and 1339 km^2 for all regions studied, contributing 89% and 11%, respectively. The west-wide rate of disturbance, 1.19% per year, is in agreement with the 1.26% per year reported by Williams *et al.* (2013) based on application of a disturbance-detection algorithm to spectral data from dense time series of Landsat scenes sampled across the west (Masek *et al.*, 2013).

These areal percentages for stand replacing harvest and fires are aggregated to assign probability values, and are applied to forest stands greater than 20 years. These simulations are performed for 100 member ensembles. The difference between ensemble-means of control and beetle scenarios is used to quantify the carbon balance impacts of bark beetles.

Results

Bark beetle induced tree/forest mortality

Data from the USFS ADS indicate the extent and distribution of damage from 2000 to 2009, causing widespread tree mortality in spruce, pine, and Douglas-fir forests from the Rocky Mountains to Pacific Coast (Fig. 2). Both the 2000-2009 average area infested by bark beetles per year, and the associated biomass killed varies by forest types and regions (see Table SI2 in supporting information). Summed across all regions, lodgepole pine MPB affects the largest area per year of 940000 ha followed by Douglas-fir beetle (120000 ha yr^{-1}), ponderosa pine MPB (80000 ha yr^{-1}), whitebark pine MPB (70000 ha yr^{-1}), Engelmann spruce beetle (68000 ha yr^{-1}) and western white pine MPB (5000 ha yr^{-1}). Summed across all forest types, RMN had the largest infested area per year of 560000 ha followed by RMS (490000 ha yr^{-1}), PNW (240000 ha yr^{-1}), and PSW (10000 ha yr^{-1}). Aggregated across all forest types, RMN had the greatest above-ground biomass mortality of 255 Gg C yr^{-1}, followed by RMS (243 Gg C yr^{-1}), PNW (179 Gg C yr^{-1}), and PSW (9 Gg C yr^{-1}). Combined across all regions, lodgepole pine MPB killed the most above-ground biomass of 510 Gg C yr^{-1}, followed by Engelmann spruce beetle (67 Gg C yr^{-1}) and Douglas-fir beetle (46 Gg C yr^{-1}) whereas western white pine MPB killed only 3 Gg C yr^{-1} during this period.

Characteristic carbon trajectories with stand age

Post-disturbance trajectories of aboveground forest stock, NPP, Rh, and NEP exhibit considerable variations with bark beetle severity (Fig. 3). As expected, increased severity results in increased biomass mortality (as shown by the drop in aboveground forest stock trajectories). After the initial drop in aboveground forest stock, the forest stand regenerates and accumulates biomass. The increase in amount of biomass killed with increased disturbance severity causes a larger spike in heterotrophic respiration and reduction in NPP, and results in a longer period required to switch from carbon source to sink as seen in the NEP trajectory. Fig. 4 shows the collection of characteristic NEP trajectories for three bark beetle disturbance severities in different forest types and forest service regions (see Fig. SI5 in appendix section for the same figure with complete NEP dip). The NEP trajectories not only vary by forest type and forest service regions but also by disturbance severity levels.

Regional carbon fluxes from recent bark beetle outbreaks

Carbon flux trends vary by region and with biomass mortality correction factors. Fig. 5 shows results aggregated across six forest types (affected by six bark beetle types) from 2000 to 2009, assuming that beetles attack stands (> 20 years old). First note that the reference case without beetle attack involves a region-wide rise in NEP for most regions. This is associated with a general recovery from a legacy of past disturbances based on stand age, and also assumes no disturbances by other agents during this period in these particular locations. Effects of beetle induced mortality are then imposed on this background sink in the case with bark beetle damage. In general, as beetle disturbed area increases from the initial year to final year in each of the plots (see Fig. 5), NEP for the case including bark beetle attacks declines in comparison to NEP without bark beetles, as heterotrophic respiration of beetle-killed biomass increases. The NEP reduction due to bark beetles includes effects of temporary reduction in NPP and also in the rise in heterotrophic respiration associated with beetle-killed biomass. Results are sensitive to biomass multipliers (recommended by Meddens *et al.* (2012), USFS experts familiar with the ADS data, and our own field-based analysis conducted at the Colorado’s Front Range), showing larger reductions in NEP with larger biomass multipliers, though we note this would tend to elevate NEP in the future by inducing a larger regrowth sink.

There is a marked difference in the cumulative NEP reduction (2000 to 2009) between the case where beetles attack all stands (> 20 years old) and the case where beetles only attack old stands (Table SI3 in supporting information). NEP is reduced more if beetles attack only old stands (compared Fig. 5 and 6) simply because the biomass killed per tree increases with stand age. Summed across all forest types, the RMN region had the largest cumulative NEP reduction of 7396 Gg C over the 10 year period considering the scenario without the biomass multiplier and assuming that bark beetles attack young and old stands alike, followed by RMS (5927 Gg C), PNW (5764 Gg C) and PSW (155 Gg C). Similar regional trends are observed assuming that bark beetles attack old (mature) stands only, RMN (7515 Gg C) had the largest cumulative reduction in NEP followed by RMS (6403 Gg C), PNW (6106 Gg C) and PSW (156 Gg C) considering the scenario without the biomass multiplier. The cumulative reduction in NEP increased for higher biomass multipliers.

Aggregated across all regions, lodgepole pine MPB had the highest cumulative NEP reduction of 12842 Gg C over the 10 year period followed by Douglas-fir beetle (3392 Gg C), and ponderosa pine MPB (1192 Gg C) whereas western white pine MPB (185 Gg C) had the least cumulative NEP reduction considering the scenario without the biomass multiplier and assuming bark beetles attack stands (> 20 years old). The magnitude of the NEP reduction among forest types increased with higher biomass multipliers. Cumulative NEP reduction over the 10 year period also increased for the case considering beetle attack old stands only, with Engelmann spruce beetle having the largest increase from 1192 Gg C to 1907 Gg C. This occurs because old stands in Engelmann spruce forests have larger biomass resulting in larger biomass killed by Engelmann spruce beetle in the old stand scenario compared to stands (> 20 years old) (Table SI2 in supporting information). The NEP of forest stands affected by bark beetle outbreaks from 2000 to 2009 generally recovered to the NEP of the control scenario by 2040 to 2060 (Fig. SI3 and SI4 in supporting information). By the year 2039 the NEP with beetle infestations approximately equals the control NEP except for cases where larger biomass is killed due to only old stands affected or larger biomass multiplier (Table SI4 in supporting information). Generally, larger values of the biomass multiplier (i.e., biomass killed), causes longer delay in the time it takes for NEP in beetle-damaged stands recover to that of their control cases (Fig. SI3 and SI4 in supporting information). Also, a larger reduction in NEP and longer time to recovery occurs in comparison to the control level, if bark beetles attack old age stands rather than any stand (> 20 years old). After full recovery (NEP due to bark beetle = control NEP), forest stands influenced by higher severity bark beetle outbreaks (having larger biomass multiplier, or attacking older stands), actively regenerate causing larger NEP increase over the control NEP level.

Aggregated across all regions and forest types, our estimates of overall regional carbon balance due to bark beetles, specified in terms of average 2000 to 2009 historical biomass killed ranges from 0.86 to 15.35 Tg C yr^{-1} ,and NEP reduction ranges from 1.92 to 3.55 Tg C yr^{-1} using the control without disturbances and 1.78 to 3.37 Tg C yr^{-1} using the control with fire and harvest disturbances depending on the stand age affected and biomass multiplier (Table 1). The effect of including future disturbances appears mainly by diminishing the long-term carbon sink toward a steady-state balance with NEP close to 0 Tg C yr^{-1} at 2050 whereas the disturbance-free scenario sustains a long-term carbon sink with NEP of about 3 Tg C yr^{-1} at 2050 as forests continue to sequester carbon in biomass stocks. The best estimates of average NEP reduction during 2000 to 2009 is 2.42 to 3.55 Tg C yr^{-1} on average using the control without disturbance and 2.26 to 3.37 Tg C yr^{-1} on average using the control with fire and harvest disturbances during the 2000 to 2009 bark beetle outbreak period, rising to 6.4 to 9.3 Tg C yr^{-1} by 2009 using the control without disturbance, and to 6.1 to 8.8 Tg C yr^{-1} using the control with fire and harvest disturbances (Table 1, Fig. 7 and Fig. 8). This is expressed as a reduction in NEP because of a prevailing background initial condition of carbon uptake in pre-disturbance forests as they grow and accumulate carbon from the legacy of prior disturbances. Regional contributions to the net carbon release were approximately 28%, 1%, 36% and 35% for the PNW, PSW, RMN and RMS regions, respectively. The reduction of NEP grew from 2000 to 2009 as the affected area grew (Fig. 7 and Fig. 8), and this decade of disturbance imposes a legacy effect of continued emissions that drops gradually over the following two decades as NPP rebounds, forests regrow, and the amount of disturbance-killed, decomposing biomass is reduced (Fig. 7 and Fig. 8). The range in beetle-induced net carbon release reflects best estimates by adopting the three- or ten-fold multiplier for the ADS reported number of trees killed in infested areas, and also assumes preferential attack of old trees as suggested strongly in the literature. This may in fact be a conservative estimate as suggested by multiple lines of evidence from our own work and also research from others. Correspondingly, the net carbon release resulting from the beetle outbreaks reported here are likely conservatively low.

Discussion

This study combines a bark beetle disturbance geospatial product, age cohort specific biomass trajectories, and an ecosystem carbon cycle model to quantify the carbon consequences of beetle outbreaks that have taken place across western US forests in the last decade. An important element that builds on our past work (Williams *et al.*, 2012) is that bark beetle disturbances are treated as partial mortality events depending on the severity of beetle infestation. The amount of biomass killed influences the shape of the carbon flux trajectories though all exhibit a general structure of transient reduction in productivity and transient increase in heterotrophic respiration due to additional beetle-killed biomass. Trajectories reported here are consistent with the typical patterns of disturbance recovery reported in the literature (e.g., Bond-

Lamberty *et al.*, 2004, Gough *et al.*, 2007, Goulden *et al.*, 2011, Law *et al.*, 2004, Litvak *et al.*, 2003, Noormets *et al.*, 2007, Pregitzer & Euskirchen, 2004) but introduce important detail about variation by forest type, disturbance severity, and region. Generally, higher severity bark beetle infestations are associated with larger initial increases in heterotrophic respiration, larger peaks in NEP, and a longer time to change from carbon source to sink. These processes occur due to the immediate post-disturbance decomposition and release of beetle-killed biomass, combined with post-disturbance vegetation regrowth. The carbon flux dependence on age differs from many other approaches that rely mainly on biome type and climate to characterize carbon fluxes.

Assessing the long term future carbon consequences of forest disturbances is highly sensitive to assumptions about recovery rates, with the possibility of slow or no recovery of forest carbon stocks. The present study assumes that recovery rates today are well represented by those in the past and that recovery of stocks following partial disturbances is similar to that inferred from inventory-based chronosequences, however this may not be the case for a few reasons. First, it is possible that severe beetle damage would lead to a change in forest type or conversion (Collins *et al.*, 2011). At present, we are limited by a lack of information for how to characterize this process in the modelling. The major implication for our results would stem from conversion to an ecosystem type that would store more or less carbon in the long-term, or a major change in the rate of carbon stock recovery. Some recent work indicates that the rate of forest (re)growth is elevated relative to that of the past as it responds to a series of global environmental changes such as increased temperatures, increased or decreased precipitation, and fertilization by carbon dioxide or nitrogen (Hember *et al.*, 2012, Williams *et al.*, 2012), but it is not clear to what degree this pattern applies to recovery following bark beetle attack.

The long term, regional carbon balance effect of forest disturbances is also highly sensitive to changes in disturbance rates. Recent studies report intensified or accelerated disturbances regimes (e.g., extent, magnitude and frequency) for both fire and insects partly associated with climate change (Raffa *et al.*, 2008, Westerling *et al.*, 2006), while harvest in the western US has been on the decline over the past three decades (Smith *et al.*, 2009). In the case of beetles, large expanses of highly productive forests have been significantly affected, and these outbreaks are expected to be more severe and expand to higher latitudes and upper elevations in the future due to climate change (Bentz *et al.*, 2010, Carroll *et al.*, 2004, Williams & Liebhold, 2002). Changes in climate could accelerate disturbance rates causing a transient net reduction in forest carbon stocks and corresponding emission to the atmosphere. Additionally, increases in disturbance rates could result in either a younger stand age distribution of the landscape, or a reduced carbon stock for a given stand age as partial disturbances by beetles shorten the residence time of live carbon in forest stands.

There are three major sources of uncertainty associated with our use of the ADS data including underestimation of forest area flown, likely underestimation of the number of trees killed, and likely overestimation of beetle affected area. The underestimation of area flown is minimized by focusing on the recent record of data covering most forest areas with some regions having full wall-to-wall coverage of flown area. The likely uncertainties due to underestimation of the number of trees killed are partially accounted for by providing two additional scenarios where biomass killed is multiplied by factors of 3 and 10 (upper estimate), in addition to reporting the scenario without any biomass correction (lower limit). The remaining uncertainties in the underestimation of the number of trees killed is accounted for by a corresponding overestimation of bark beetle infested area, such that the two categories of uncertainties cancel out when we prescribe their effects on the carbon cycle. In addition to the three major data source uncertainties, another uncertainty relates to the conversion of number of trees killed to biomass killed by bark beetles. ADS data reported the number of trees affected by bark beetles per area, and is converted to biomass affected per area using relatively coarse county-level data on average biomass per tree. The average biomass killed per tree by bark beetle depends on the structure (i.e., size and age) of forest stands attacked. Larger and older stands are highly susceptible to bark beetle attacks compared to younger and actively regenerating ones (Schmid & Frye, 1976, Weatherby & Thier, 1993), but the relative proportions of size and age affected is uncertain as it depends on other factors, such as, severity and extent of outbreak, and pre-disturbance legacies (Kulakowski *et al.*, in press). This has important consequences for our carbon balance and flux estimates.

Overall, we estimate average per year historical biomass kill by beetles ranging 4.61 to 15.35 Tg C yr^{-1}, and average historical NEP reduction ranging 2.42 to 3.55 Tg C yr^{-1} using the control without disturbance or 2.26 to 3.37 Tg C yr^{-1} using the control with fire and harvest disturbances during 2000 to 2009 bark beetle outbreak period. The response peaks at a net reduction of NEP of about 6.1 to 9.3 Tg C yr^{-1} by 2009. These best estimates adopt the 3 to 10 fold multiplier for biomass killed in infested areas and assume preferential attack of old trees as suggested strongly in the literature (Shore & Safranyik, 1992). A large difference in NEP reduction does not exist compared to the relative magnitude of biomass multipliers of 3 and 10 because the killed-carbon is released slowly and thus contributes to only small per year differences in NEP though a cumulative sum over the NEP legacy recovers the full difference between scenarios. Calibration and validation of the ADS data on the area and severity of beetle outbreaks is the single most important component needed for uncertainty reduction with our method, followed by improved clarity about the age of beetle attacked trees.

Prior studies have shown that bark beetles have major regional consequences on the carbon balance. One of the first was by Kurz *et al.* (2008) reporting on the sizeable beetle outbreaks of British Columbia. They estimated that mountain pine beetle outbreaks caused a reduction in NEP of 13.46 Tg C yr^{-1} from 2000 to 2020 including a sink to source conversion in British Columbia. The total biomass mortality we estimated for US outbreaks is approximately half as large as that in the British Columbia case, and the NEP reduction is correspondingly lower than that reported by Kurz *et al.* (2008). This is true despite similar areas of mortality. There are multiple factors that contribute to this difference. First, the uniform pine dominated stands attacked in Canada experienced higher mortality and was also in higher-biomass forests on average as noted by Hicke *et al.* (2013). The difference in estimates can also be attributed to the increasing historical disturbance rate until 2006 analyzed by the Kurz *et al.* (2008) study followed by a sustained, slowly declining disturbance rate projected until 2020, whereas in this study the NEP reduction is calculated from the historical 2000 to 2009 time period only without projecting impacts into the future and thus transpires over only one decade instead of the two decades simulated in the Kurz *et al.* (2008) study.

Hicke *et al.* (2013) also reported sizeable carbon impacts from bark beetles, reporting annual mean tree kill from beetles of 2 to 24 Tg C yr^{-1} (best estimate of 21 Tg C yr^{-1}) from 1997 to 2010 and for the same western US region studied here. Our results are in broad agreement, being spanned by their range, but yield an upper-end best estimate (15 Tg C yr^{-1}) that is somewhat lower. Their study differed from ours in a few important ways. First, they translated the aerial survey maps of the number of beetle killed trees per hectare by converting this to mortality area knowing crown diameters from the larger trees that beetles tend to attack and then adjusting this (upwards) based on comparison to fine resolution remote sensing imagery (Meddens *et al.*, 2012). Second, their study estimated the carbon in killed trees by intersecting their mortality area map with a forest biomass map by Blackard *et al.* (2008), produced with forest inventory and MODerate Imaging Spectroradiometer (MODIS) data. Hicke *et al.* (2013) screened out all pixels known to have been disturbed by moderate to high severity fires and then determined a representative mean carbon stock in undisturbed locations by ecoregion and forest type, lastly selecting the maximum of the carbon stock from this mean or that from the Blackard *et al.* (2008) dataset. Lastly, the Hicke *et al.* (2013) study included a broader range of bark beetle types and hence a larger area, such as the Pinyon-Juniper woodlands that have experienced attack from the Pinyon ips beetle that was not included in our work.

It is instructive to compare the carbon balance impacts of bark beetles to that from other global change factors affecting western US forests today. In past work we estimated that fires killed 20 Tg C yr^{-1} of biomass on average from 1996 to 2008, with about 37%, or 7 Tg C yr^{-1}, released to the atmosphere as direct combustion (Ghimire *et al.*, 2012). Thus, carbon impacts of the recent beetle outbreaks are of comparable magnitude to that from fires across the western US. Though harvesting has slowed in recent decades, it remains widespread in the region, removing about 30 Tg C yr^{-1} from forests during the 1990s and 2000s (EPA, 2008), and leaving about 20 Tg C yr^{-1} to decompose on site post-harvest in the form of dead leaves, roots, branches and stems

(Williams *et al.*, 2012). This suggests that beetle outbreaks in the western US during the 2000s killed about 30% as much biomass as was killed by harvests over the same time frame.

Another point of comparison comes from forest inventories, which indicate a net annual increase in forest carbon stocks of about 170 Tg C for the entire US (EPA, 2008). This goes above and beyond the 130 Tg C yr^{-1} removed by harvesting plus 20 Tg C yr^{-1} from fires, indicating a forest NEP of about 320 Tg C yr^{-1}. Recent work suggests that about half of this net uptake in forests derives from a legacy of regrowth following past disturbances, particularly harvests, while the other half would appear to be due to some combination of growth enhancement factors such as elevated carbon dioxide levels, nitrogen fertilization, or forest management activities (Williams *et al.*, 2012). Meanwhile, past harvesting has left an emissions legacy from wood products which offsets some or all of the net uptake due to regrowth by leaking about 100 Tg C annually (EPA, 2008). This effectively degrades the NEP uptake in forests, and can be counted against the regrowth legacy of about 160 Tg C yr^{-1} (from dividing 320 Tg C yr^{-1} in half), leaving roughly 60 Tg C yr^{-1} as a sink due to forest recovery. With the western US states studied here accounting for about half of the total US forest sink, we estimate a forest regrowth sink of about 30 Tg C yr^{-1} from past disturbances. By comparison, mortality caused by bark beetle outbreaks from 2000 to 2009 (15 Tg C yr^{-1}) amounts to about half of the regrowth sink in western forests. Lastly, the 150 Tg C cumulative effect of beetles over the 2000s is close to 10% of one year's worth of US-wide carbon emissions from fossil fuel combustion (=1563 Tg C in 2005) (EPA, 2008).

Several productive lines of future research exist which can complement and build on this work. First, precise estimates of bark beetle affected area and biomass mortality, as well as stand size and age susceptibility especially at regional levels are needed to reduce the uncertainty in our carbon balance estimates. Second, our study considered the impact of six bark beetles types, and a more comprehensive understanding of bark beetle dynamics on carbon balance would need to consider more bark beetles types, for example the Pinyon ips beetle that is devastating Pinyon pines (Hicke *et al.*, 2013, Meddens *et al.*, 2012), and also other insect types (e.g., defoliators, and pathogens). Third, a more complete analysis of disturbance impacts on carbon budget needs to compare and evaluate the impacts of disturbances, such as, fires, bark beetle, and harvests, as well as episodic climatic events, such as, droughts and heat stress. Fourth, there is a need to forge new understanding on the relative contributions of disturbance, growth enhancement factors, and climate variability and trends on the regional carbon balance in United States forests.

In conclusion, our study presents the estimates of the carbon consequences of bark beetles at a regional scale across the western United States. The regional impacts of bark beetle outbreaks are dependent on area affected and biomass killed which can be derived from aerial detection surveys conducted across landscape level scales. These regional carbon consequences vary by forest and bark beetle types, regions, disturbance severity levels and stand ages. In this study, the best estimates of average per year overall historical biomass killed due to six types of bark beetles across forests of western United States ranges from 5 to 15 Tg C yr^{-1}, and historical NEP reduction ranges from 6.1 to 9.3 Tg C yr^{-1} by 2009. These best estimates reflect the findings of our own field-based observations, suggestions of the ADS experts and results of the recent literature that we need a biomass mortality multiplier, and also incorporate findings from the literature that old stands are attacked preferentially. Uncertainties in our estimates are related to a lack of detailed field surveys, calling out the need forimproved characterization of the extent and severity of individual bark beetle outbreaks across the western US forests. The carbon legacy of present bark beetle disturbances will continue into the future, and our study estimates that the legacy of 2000-2009 outbreaks will remain until 2040-2060.

Acknowledgements: B.G., C.A.W., G.J.C., and J. M. thank the NASA Terrestrial Ecology program for financial support under grant NNX10AR68G. Additionally, M.V. received financial support from the 2011-2013 NASA Earth and Space Science Fellowship (NESSF) (11-Earth11F-134 and 12-Earth12R-59).

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Supporting information legends

SI.1 Derivation of characteristic post-disturbance carbon flux trajectories

SI.2 Quantifying recent beetle-induced mortality

SI.3 Quantifying carbon consequences of recent outbreaks

Table 1. Overall regional carbon balance associated with bark beetles in comparison to other studies.

Source	Region	Time period	Biomass Multiplier	Stand Age	Above-ground Biomass Killed (Tg C yr^{-1})	Biomass Killed[1] (Tg C yr^{-1})	NEP Reduction[2] (Tg C yr^{-1})
Carbon consequences of historical bark beetle infestations							
This study	Western US	2000-2009	None	Age > 20	0.69	0.86	1.78 - 1.92
This study	Western US	2000-2009	3	Age > 20	2.06	2.57	2.03 - 2.17
This study	Western US	2000-2009	10	Age > 20	6.86	8.57	2.86 - 3.02
This study	Western US	2000-2009	None	Old Stands	1.23	1.54	1.87 - 2.02
This study	Western US	2000-2009	3	Old Stands	3.68	4.61	2.26 - 2.42
This study	Western US	2000-2009	10	Old Stands	12.28	15.35	3.37 - 3.55
Kurz *et al.* (2008)	Canada	2000-2006	None		22.69*		
Kurz *et al.* (2008)	Canada	2000-2020	None				13.46

Incorporating all uncertainties, the overall estimates of historical biomass killed (averaged from 2000 to 2009) ranges from 0.86 to 15.35 Tg C yr^{-1} and historical NEP reduction (averaged from 2000 to 2009) ranges from 1.78 to 3.55 Tg C yr^{-1}.

Best estimates of historical biomass killed (averaged from 2000 to 2009) ranges from 4.61 to 15.35 Tg C yr^{-1} and historical NEP reduction (averaged from 2000 to 2009) ranges from 2.26 to 3.55 Tg C yr^{-1} from bark beetle outbreaks because literature, field measurements and ADS experts suggest we need a biomass multiplier, and literature suggests old stands are attacked preferentially.

[1] Biomass killed includes both above- and below-ground biomass killed. Below-ground biomass killed is calculated from above-ground biomass killed assuming a below- to above-ground

biomass ratio of 0.25 which is consistent for temperate forest conifers as reported in IPCC (2006) and Mokany and others (2006).

[2] NEP reduction is the average yearly reduction due to bark beetles infestations for the duration of study specified in the time period column. The lower range in NEP reduction in each row of the table uses a control with fire and harvest disturbances, and the upper range in NEP reduction uses a control without disturbance.

[*] Assumes that the stemwood biomass in Kurz *et al.* (2008) corresponds to aboveground biomass in this study, and is estimated using merchantable stemwood volume and specific gravity of 0.397 as reported in Kurz *et al.* (2008).

Figure legends

Figure 1. Schematic of the methodology for integrating CASA model with forest inventory data to estimate the carbon flux trajectories and regional carbon balance.

Figure 2 Spatial distribution of the major bark beetle types in the western United States. Abberviations in the map legend are as follows: MPB is mountain pine beetle, LdP is lodgepole pine, PP is ponderosa pine, WBP is whitebark pine and WWP is western white pine.

Figure 3. Post Douglas-fir bark beetle trajectories for a) aboveground forest stock, b) NPP, c) heterotrophic respiration, and d) NEP in PNW high productivity forests. Bark beetle infested Douglas-fir in PNW are selected as an example showing how we generate post-disturbance NPP, respiration and NEP trajectories from the post-disturbance biomass trajectories. The low, medium and high severity refers to three different examples of bark beetle disturbances that kill low, medium and high amounts of biomass, respectively as depicted by the drop in aboveground forest stock at years since disturbance value of 0 in the figure.

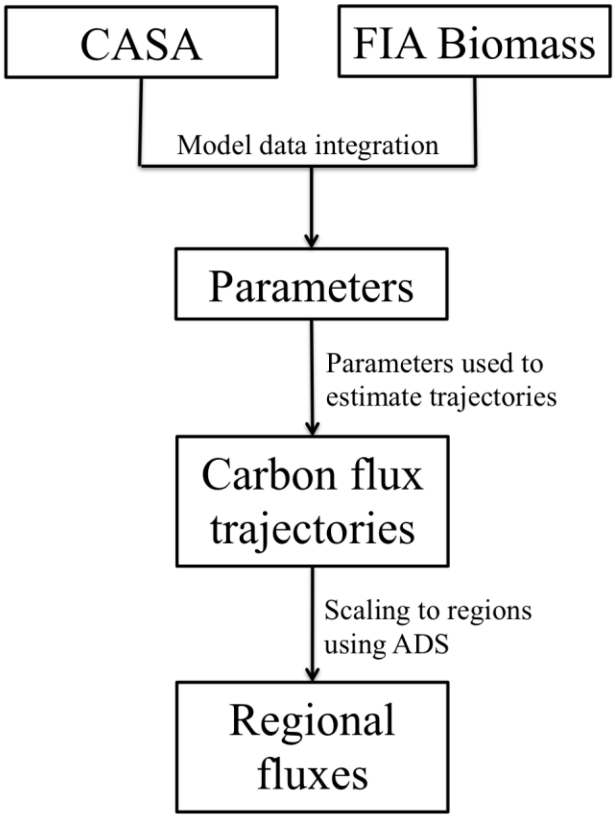
Figure 4. Characteristic NEP trajectories for different bark beetle severity levels across forest types and forest service regions.

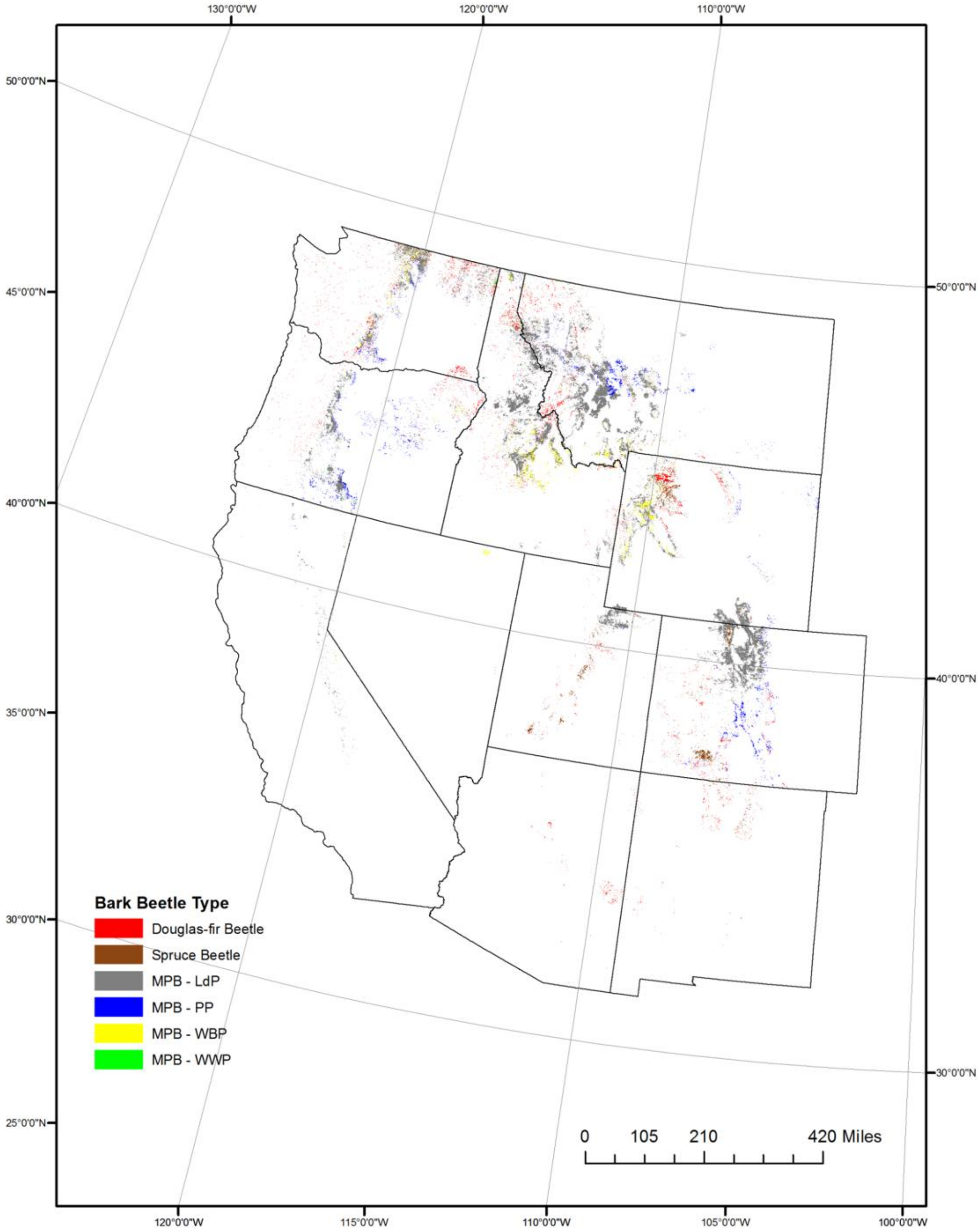
Figure 5. Regional carbon flux trends in the presence and absence of bark beetle infestations in bark beetle affected areas from 2000 to 2009 aggregated across six forest types for different combinations of regions and biomass mortality multipliers assuming that beetles attack stands of age larger than 20 years.

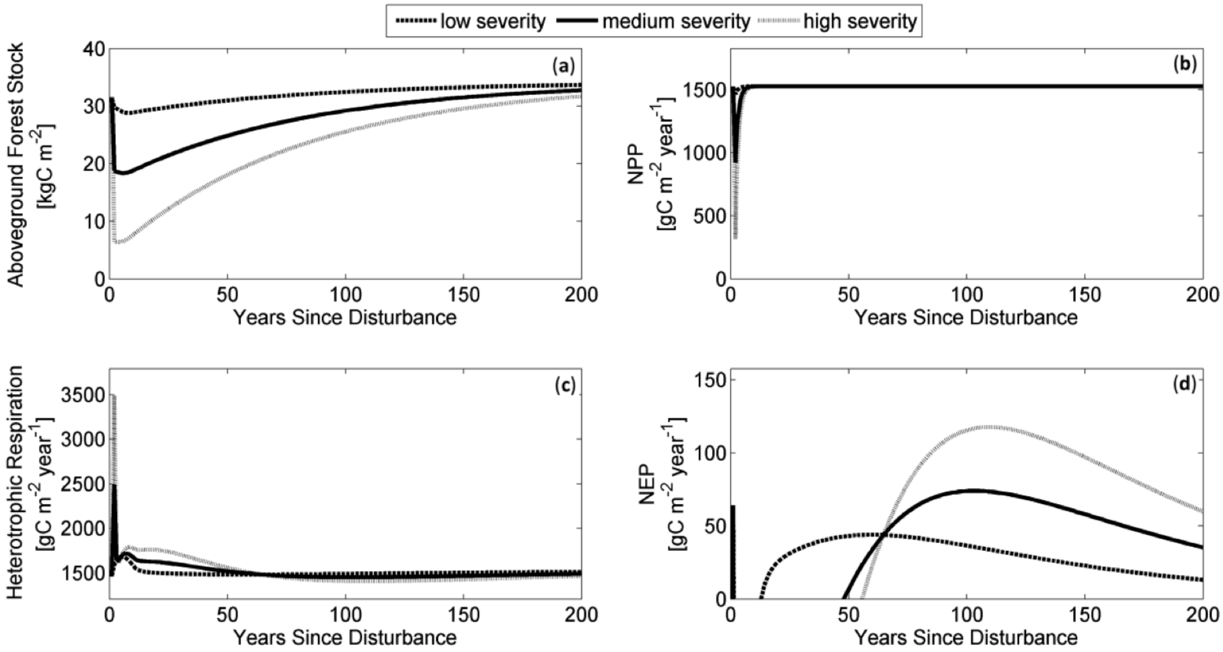
Figure 6. Same as in Figure 4 but assuming that beetles attack only old forest stands defined as stands with stand age larger than 120 and 80 years, for Douglas-fir beetle and MPB attacks respectively, and diameter larger than 16 inches for spruce beetles attacks.

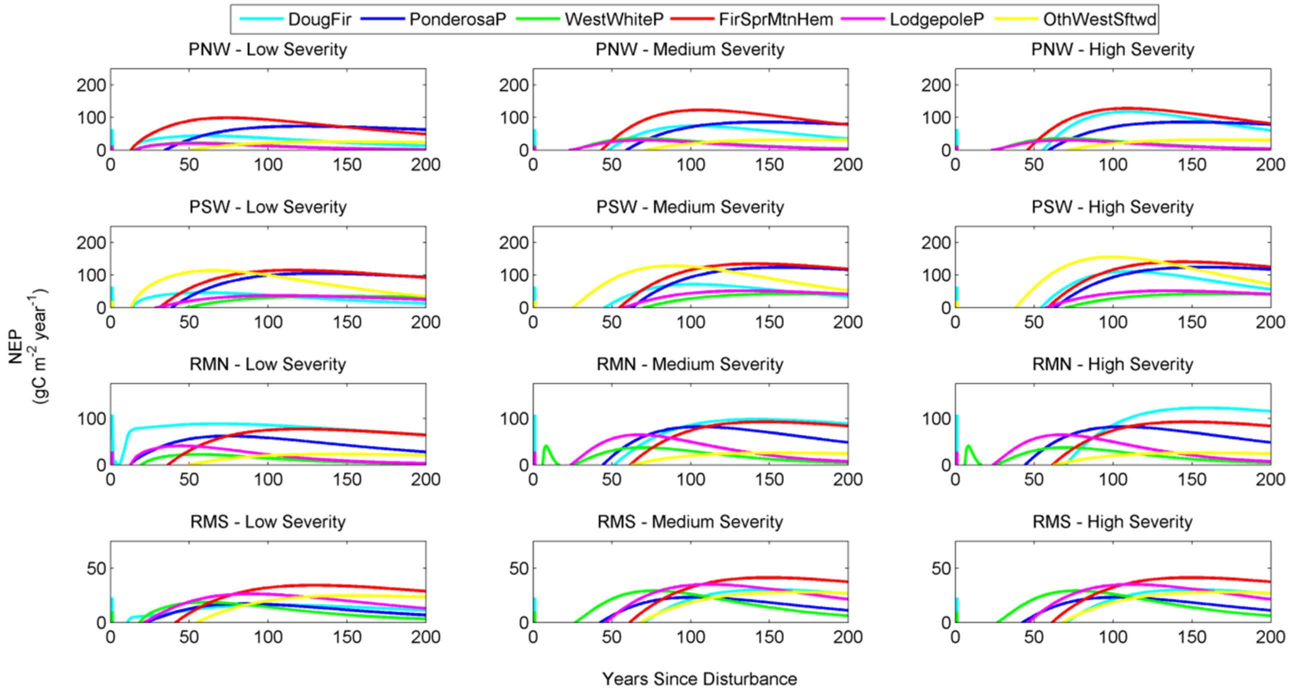
Figure 7. Carbon flux impacts of historical bark beetle outbreaks from 2000 to 2009: a) NEP and b) NEP reduction, assuming that beetles attack only old forest stands using control without disturbance. The carbon fluxes are for immediate and legacy impacts of historical bark beetle infested areas across western US forests, and bark beetle disturbances are not projected into the future beyond year 2009.

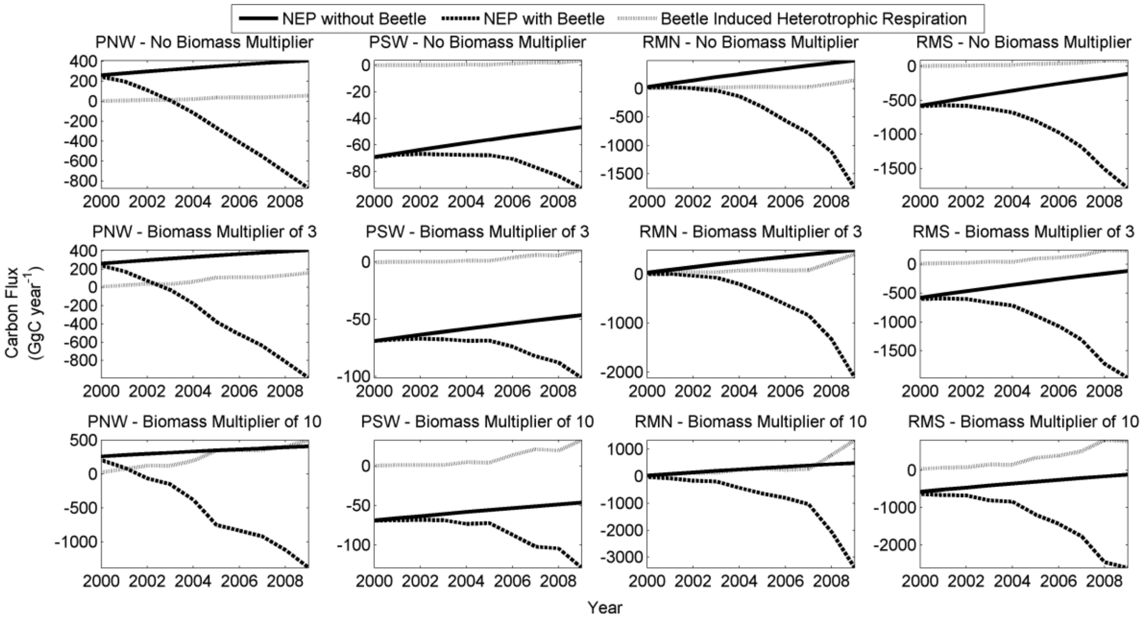
Figure 8. Carbon flux impacts of historical bark beetle outbreaks from 2000 to 2009: a) NEP and b) NEP reduction, assuming that beetles attack only old forest stands using control with fire and harvest disturbances. The carbon fluxes are for immediate and legacy impacts of historical bark beetle infested areas across western US forests, and bark beetle disturbances are not projected into the future beyond year 2009.

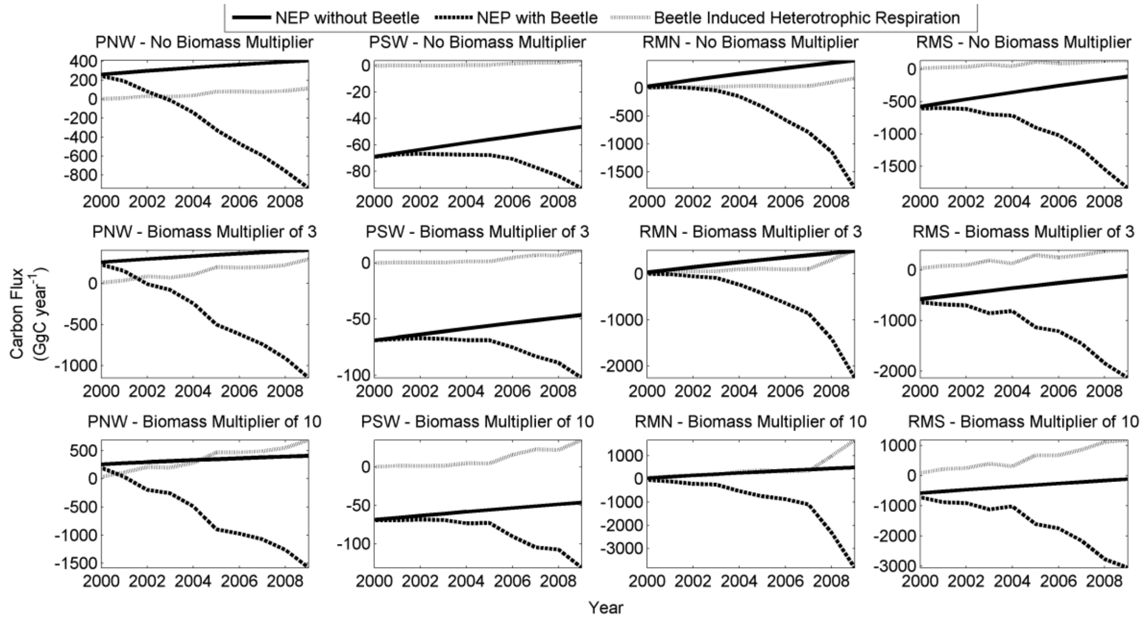

CASA
FIA Biomass
Model data integration
Parameters
Parameters used to estimate trajectories
Carbon flux trajectories
Scaling to regions using ADS
Regional fluxes

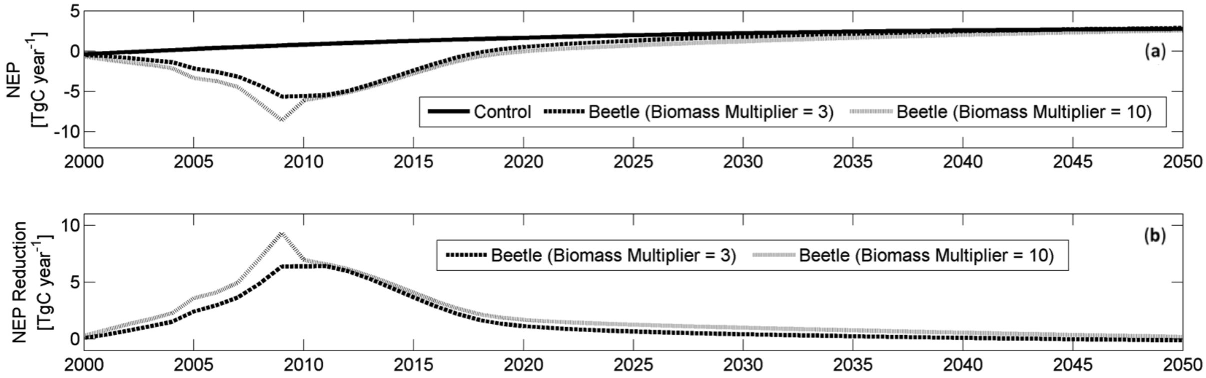

130°0'0"W
120°0'0"W
110°0'0"W
50°0'0"N
45°0'0"N
40°0'0"N
35°0'0"N
30°0'0"N
25°0'0"N
50°0'0"N
40°0'0"N
30°0'0"N
Bark Beetle Type
Douglas-fir Beetle
Spruce Beetle
MPB - LdP
MPB - PP
MPB - WBP
MPB - WWP
0
105
210
420 Miles
120°0'0"W
115°0'0"W
110°0'0"W
105°0'0"W
100°0'0"W

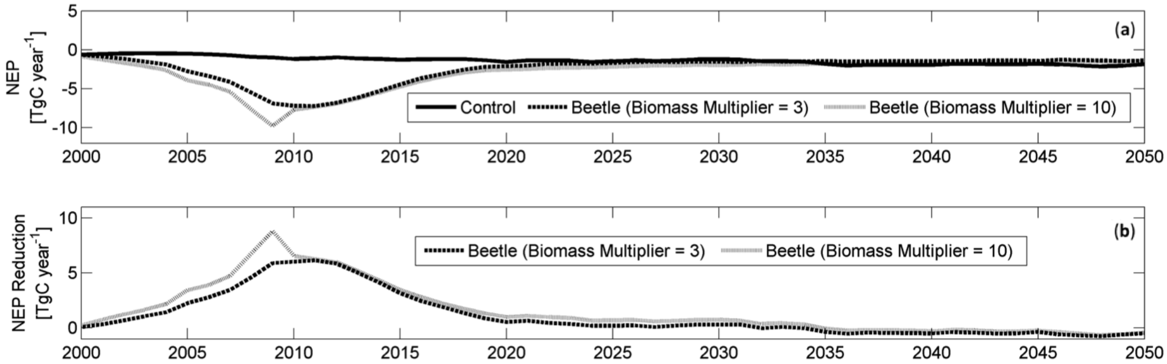

low severity
medium severity
high severity
(a)
Aboveground Forest Stock [kgC m^{-2}]
Years Since Disturbance
(b)
NPP [gC m^{-2} year^{-1}]
Years Since Disturbance
(c)
Heterotrophic Respiration [gC m^{-2} year^{-1}]
Years Since Disturbance
(d)
NEP [gC m^{-2} year^{-1}]
Years Since Disturbance


DougFir
PonderosaP
WestWhiteP
FirSprMtnHem
LodgepoleP
OthWestSftwd
PNW - Low Severity
PNW - Medium Severity
PNW - High Severity
PSW - Low Severity
PSW - Medium Severity
PSW - High Severity
RMN - Low Severity
RMN - Medium Severity
RMN - High Severity
RMS - Low Severity
RMS - Medium Severity
RMS - High Severity
NEP (gC m^{-2} year^{-1})
Years Since Disturbance


NEP without Beetle
NEP with Beetle
Beetle Induced Heterotrophic Respiration
PNW - No Biomass Multiplier
PSW - No Biomass Multiplier
RMN - No Biomass Multiplier
RMS - No Biomass Multiplier
PNW - Biomass Multiplier of 3
PSW - Biomass Multiplier of 3
RMN - Biomass Multiplier of 3
RMS - Biomass Multiplier of 3
PNW - Biomass Multiplier of 10
PSW - Biomass Multiplier of 10
RMN - Biomass Multiplier of 10
RMS - Biomass Multiplier of 10
Carbon Flux (GgC year^{-1})
Year
2000 2002 2004 2006 2008


NEP without Beetle
NEP with Beetle
Beetle Induced Heterotrophic Respiration
PNW - No Biomass Multiplier
PSW - No Biomass Multiplier
RMN - No Biomass Multiplier
RMS - No Biomass Multiplier
PNW - Biomass Multiplier of 3
PSW - Biomass Multiplier of 3
RMN - Biomass Multiplier of 3
RMS - Biomass Multiplier of 3
PNW - Biomass Multiplier of 10
PSW - Biomass Multiplier of 10
RMN - Biomass Multiplier of 10
RMS - Biomass Multiplier of 10
Carbon Flux (GgC year^{-1})
Year
2000 2002 2004 2006 2008


NEP
[TgC year^{-1}]
5
0
-5
-10
(a)
Control
Beetle (Biomass Multiplier = 3)
Beetle (Biomass Multiplier = 10)
2000
2005
2010
2015
2020
2025
2030
2035
2040
2045
2050
NEP Reduction
[TgC year^{-1}]
10
5
0
(b)
Beetle (Biomass Multiplier = 3)
Beetle (Biomass Multiplier = 10)
2000
2005
2010
2015
2020
2025
2030
2035
2040
2045
2050


NEP
[TgC year^{-1}]
5
0
-5
-10
(a)
Control
Beetle (Biomass Multiplier = 3)
Beetle (Biomass Multiplier = 10)
2000
2005
2010
2015
2020
2025
2030
2035
2040
2045
2050
NEP Reduction
[TgC year^{-1}]
10
5
0
(b)
Beetle (Biomass Multiplier = 3)
Beetle (Biomass Multiplier = 10)
2000
2005
2010
2015
2020
2025
2030
2035
2040
2045
2050