

Regional carbon cycle responses to 25 years of variation in climate and disturbance in the US Pacific Northwest

David P. Turner¹ · William D. Ritts¹ · Robert E. Kennedy² · Andrew N. Gray³ · Zhiqiang Yang¹

Received: 9 September 2015 / Accepted: 9 March 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Variation in climate, disturbance regime, and forest management strongly influence terrestrial carbon sources and sinks. Spatially distributed, process-based, carbon cycle simulation models provide a means to integrate information on these various influences to estimate carbon pools and flux over large domains. Here we apply the Biome-BGC model over the four-state Northwest US region for the interval from 1986 to 2010. Landsat data were used to characterize disturbances, and forest inventory data were used to parameterize the model. The overall disturbance rate on forest land across the region was 0.8 % year⁻¹, with 49 % as harvests, 28 % as fire, and

23 % as pest/pathogen. Net ecosystem production (NEP) for the 2006–2010 interval on forestland was predominantly positive (a carbon sink) throughout the region, with maximum values in the Coast Range, intermediate values in the Cascade Mountains, and relatively low values in the Inland Rocky Mountain ecoregions. Localized negative NEPs were mostly associated with recent disturbances. There was large interannual variation in regional NEP, with notably low values across the region in 2003, which was also the warmest year in the interval. The recent (2006–2010) net ecosystem carbon balance (NECB) was positive for the region (14.4 TgC year⁻¹). Despite a lower area-weighted mean NECB, public forestland contributed a larger proportion to the total NECB because of its larger area. Aggregated forest inventory data and inversion modeling are beginning to provide opportunities for evaluating model-simulated regional carbon stocks and fluxes.

Editor: Wolfgang Cramer.

Electronic supplementary material The online version of this article (doi:10.1007/s10113-016-0956-9) contains supplementary material, which is available to authorized users.

✉ David P. Turner
david.turner@oregonstate.edu

William D. Ritts
david.ritts@oregonstate.edu

Robert E. Kennedy
robert.kennedy@oregonstate.edu

Andrew N. Gray
andy.gray@oregonstate.edu

Zhiqiang Yang
zhiqiang.yang@oregonstate.edu

¹ Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA

² College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

³ USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331, USA

Keywords Pacific Northwest · Carbon · Climate · Disturbances · Net ecosystem production · Net ecosystem carbon exchange

Introduction

The mass balance approach to evaluating the global carbon cycle estimates the net land flux as the residual between fossil fuel emissions and the sum of carbon accumulation in the atmosphere and in the ocean (Le Quere et al. 2014). That approach suggests that the terrestrial biosphere is a significant sink for atmospheric carbon dioxide (CO₂). The estimate for 2013 is for a terrestrial biosphere sink of 2.5 ± 0.5 PgC year⁻¹, which offsets 23 % of anthropogenic emissions (GCP 2015). However, to better understand the terrestrial carbon cycle, and to evaluate the

possibilities for increased carbon sequestration, there is wide interest in quantifying carbon fluxes at more local and regional scales (Lu et al. 2013). Carbon flux can be monitored at the ecosystem scale with the eddy covariance approach (Baldocchi et al. 2001), or repeated biometric inventories (Curtis et al. 2002). However, at the intermediate scales of landscape, ecoregion, and region, evaluating carbon flux is more difficult and uncertain. Spatial heterogeneity in climate, soils, disturbance regime, and forest management, as well as temporal variation in weather all contribute to variation in carbon sources and sinks (Lu et al. 2013; Turner et al. 2015a).

Process-based carbon cycle simulation models (Liu et al. 2011) provide a means to estimate carbon pools and flux at these intermediate scales (Turner et al. 2004). Scaling of carbon stocks and flux by way of a simulation model offers a synoptic view of the carbon cycle and permits assessment of the relative strength of alternative carbon cycling pathways. These models are used in efforts to understand the carbon cycle (Thornton et al. 2002) because they can assimilate a wide array of observational data, and they permit investigation of the mechanisms underlying reported carbon fluxes. Here we implement a spatially distributed carbon cycle process model over the four-state (Oregon, Washington, Idaho, and Western Montana) Northwest US region for the interval from 1986 to 2010. Our goal was an improved understanding of spatial and temporal heterogeneity in regional- and ecoregion-scale carbon stocks and flux.

The northwest region is undergoing multiple changes in climate and vegetation relevant to the carbon cycle (Law and Waring 2015). A trend of climate warming over recent decades is observed in meteorological station data (e.g., Barnett et al. 2008; Pederson et al. 2010) albeit with controversy about the relative influence of internal climate variability versus anthropogenic factors (Abatzoglou et al. 2014; Johnstone and Mantua 2014; Mote 2003) and possible artifacts in the observational record (Oyler et al. 2015). Observations and modeling of the hydrologic cycle suggest progressively decreasing snow historically (Barnett et al. 2008; Mote 2006), which means an earlier onset of dry soils in the summer. A $\sim 25\%$ increase in atmospheric CO_2 since 1960 is likely increasing productivity (Soule and Knapp 2013) and decreasing transpiration (Keenan et al. 2013). Rates of tree mortality from all causes are increasing over much of the Western USA (van Mantgem et al. 2009). The forest disturbance regime in the northwest region is characterized by an increasing incidence of wildfire (Littell et al. 2009; Turner et al. 2015a), generally attributed to climate warming. Pest/pathogen outbreaks are likewise increasing (Hicke et al. 2013), again associated with warming (Preisler et al. 2012).

These changes impact the carbon cycle in direct and indirect ways (Liu et al. 2011). Interannual variation in climate affects forest productivity (Beedlow et al. 2013) as well as the rate of heterotrophic respiration (Hibbard et al. 2005). The impacts of disturbances on the carbon cycle include direct emissions associated with wildfire (Campbell et al. 2007) and delayed emissions associated with decomposition of snags (i.e., standing dead) and residual coarse woody debris (Hicke et al. 2013; Meigs et al. 2011). The drought in the Western USA from 2000 to 2004 strongly reduced the background carbon sink (Schwalm et al. 2012). Aboveground live carbon stocks in California are believed to have declined from 2001 to 2010, mostly because of wildfire (Gonzalez et al. 2015). In contrast, the implementation of the Northwest Forest Plan in the western parts of Oregon and Washington (Thomas et al. 2006) has contributed to an increase in carbon stocks on public forestland (Gray and Whittier 2014; Turner et al. 2011a).

The ecoregions of the Pacific Northwest are distinct with respect to climate, soil, and vegetation (USGS 2015); thus, our effort to differentiate them in relation to recent carbon cycle changes is warranted. A further breakout by public versus private ownership is also of interest because of the large ownership-based differences in forest management (Garman et al. 1999).

Methods

Overview

This study is a region-wide extension of a previous ecoregion-scale-based analysis, and more detail is available on methods in Turner et al. (2015a). The general approach is based on application of the Biome-BGC carbon cycle process model in a spatially distributed mode (i.e., run cell-by-cell over a grid). The approach relies on three key datasets. Satellite remote sensing (Landsat) is used to characterize the land cover and disturbance regime. Distributed meteorological station data are used to drive the algorithms in Biome-BGC for photosynthesis, autotrophic respiration, heterotrophic respiration, and evapotranspiration. Lastly, observations at a network of USDA Forest Service Forest Inventory and Analysis (FIA) plots (Woudenberg et al. 2010) are used to calibrate and evaluate the carbon stocks and flux estimates.

The model

Biome-BGC is a daily time step ecosystem process model that treats the carbon, nitrogen, and hydrologic cycles

(Thornton et al. 2002). It is prognostic with respect to foliar biomass, thus capable of simulating seasonal foliage cycles, as well as the full successional cycle in forest ecosystems. We have adapted the model to run in croplands (Turner et al. 2007) and to simulate disturbance and recovery associated with forest harvest (Law et al. 2004), wildfire (Meigs et al. 2011), and pests/pathogens (Turner et al. 2015a). Mass balance is maintained by transfers among C pools and to the atmosphere at the time of a disturbance. Biome-BGC requires specification of 20 parameters (White et al. 2000), and example parameter values by biome type are given in (Turner et al. 2007). For the evergreen needleleaf forest cover type, which dominates much of the northwest, two parameters (annual mortality fraction and the fraction of nitrogen as rubisco) were optimized at the ecoregion scale based on FIA plot data (see below).

The 2010 land cover over a 25-m grid (Fig. 1) was from the National Land Cover Database (NLCD 2006) and was based on Landsat data. The ecoregion boundaries (SFig. 1) were from (Omernik 1987), and descriptions of the ecoregions are given in US Geological Survey document (USGS 2015). Ownership boundaries (SFig. 2) were from the Gap Analysis Program (GAP 2014). A model run consists of a spin-up, to bring slow turnover carbon pools (e.g., soil) into near equilibrium with the local climate, followed by one or two disturbance events (identified by year, type, magnitude, and duration). To limit the number of simulations required, only the 10 most frequent combinations of cover type and disturbance history in each 1 km² grid cell were run. Area-weighted mean values were then reported for carbon stocks and fluxes by year. Over 90 % of the original study area was covered with this approach.

Disturbance events

For the forest cover type, the disturbance history of each 25 m grid cell was specified based on Landsat observations. We assembled a time series (1985–2011) of Landsat images (one per year) over all forest areas and evaluated the trajectories and inflection points of a spectral vegetation index for each 25 m pixel (Kennedy et al. 2010, 2012; Meigs et al. 2015). The disturbance type was classified as harvest, fire, or pest/pathogen. Abrupt disturbances (i.e., a sharp drop in the vegetation index) were classified as fire if they overlapped with the Monitoring Trends in Burn Severity dataset (MTBS 2015), and otherwise as harvest. Nonabrupt disturbances were classified as pest/pathogen, and the remote sensing observations indicated a beginning year and a year of maximum impact. A class (bin) for disturbance magnitude and a class for duration were associated with each disturbance event (Turner et al. 2015a), and for reporting purposes, the year of the event was assigned to the year of maximum magnitude. Disturbances previous to 1985 were based on stand age (SFig. 3), also estimated from Landsat data using Gradient Nearest Neighbor (GNN) analysis (Ohmann and Gregory 2002). GNN-based stand age was not available for Idaho and Montana, so spectral relationships of Landsat data and stand age in eastern Oregon and Washington were used (with reference to the observed age class distributions from FIA data in Idaho and Montana) to estimate stand age in those states.

Other model inputs

The 25-year time series of daily meteorological fields (solar radiation, precipitation, maximum temperature,

Fig. 1 Land cover in the study domain

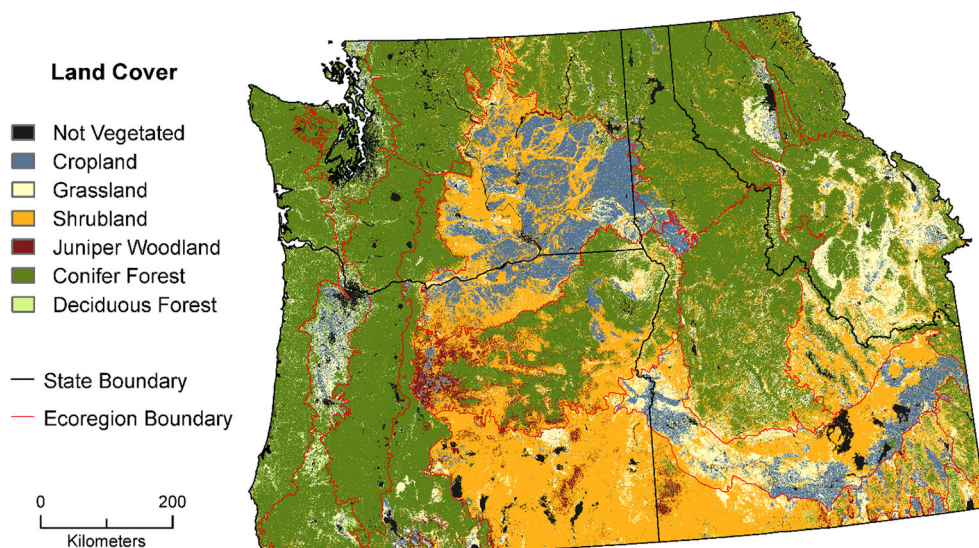
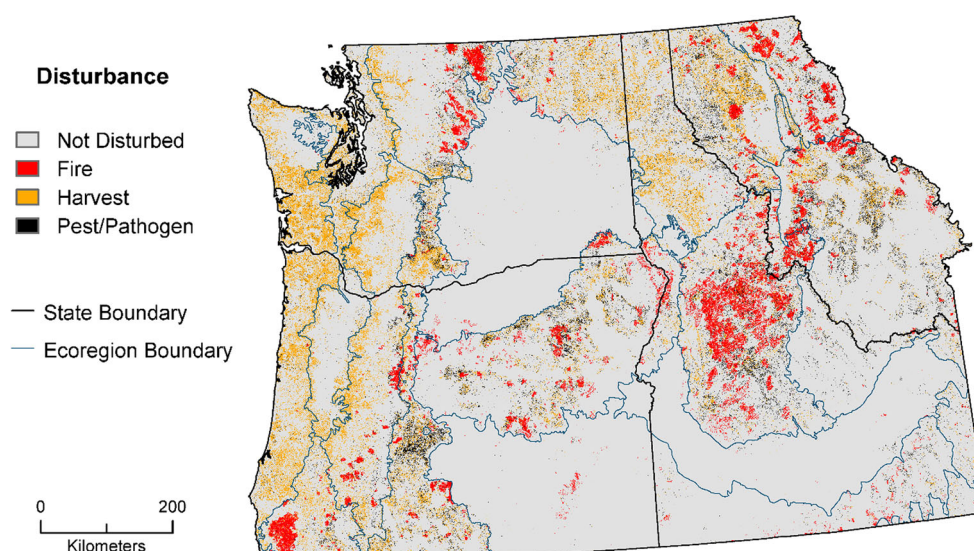


Fig. 2 Location of all disturbances (1986–2010)**Table 1** Proportional area disturbed per year by ecoregion

Ecoregion	Mean percentage of forest/year		
	Harvest	Fire	Pest/pathogen
CR	1.090	0.003	0.098
PL	0.870	0.000	0.138
WV	1.050	0.002	0.123
KM	0.507	0.629	0.112
NC	0.315	0.352	0.064
WC	0.587	0.107	0.089
EC	0.579	0.165	0.399
BM	0.248	0.344	0.316
NR	0.634	0.104	0.148
IB	0.240	0.897	0.187
CA	0.210	0.700	0.122
MR	0.310	0.215	0.112

See SFig. 1 to link ecoregion acronyms to ecoregion names and locations

minimum temperature, and vapor pressure deficit) at 1 km resolution (SFig. 4) was from Oak Ridge National Laboratories (ORNL 2014). These data were developed by interpolation of meteorological station data using digital elevation maps and general meteorological principles (Thornton et al. 1997; Thornton et al. 2014). Soil depth and texture were from a conterminous US dataset (CONUS 2007).

Forest inventory data

The FIA plot network (a 5-km grid over all forested area) was used for parameter optimization. In each forest-dominated ecoregion (subdivided by state where relevant), the

model was run at all plot locations (approximated to within 500 m) over a range of values for the annual mortality and fraction of leaf nitrogen as rubisco parameters. Stand age was set to the year specified in the plot data. Parameter selection was based on comparisons of observed and simulated aboveground biomass (e.g., SFig. 5).

Results

Climate

The most characteristic geographic feature of the climate in the northwest is the west-to-east gradient from a maritime climate along the Pacific Ocean Coast, with moderate temperatures and relatively high annual precipitation, to a more continental climate associated with the inland Rocky Mountains, having colder winter temperatures and more summer precipitation (SFig. 4). There is not a strong trend in the regional climate over the 1985–2011 study interval, but there is considerable interannual variation (SFig. 6).

Disturbance regime

The overall disturbance rate on forestland across the region was 0.8 % year⁻¹, with 49 % as harvests, 28 % as fire, and 23 % as pest/pathogen (Fig. 2). A large proportion of the harvested area was on private forestland (62 %). Proportional harvest rates on private land decreased going from west to east from 1.09 % year⁻¹ in the CR ecoregion, to 0.59 % year⁻¹ in WC, and 0.31 % year⁻¹ in the MR ecoregion (Table 1). The harvest rate was consistently less than 0.50 % year⁻¹ on public forest land. The area of high-intensity harvest per year declined on public land over the

study interval, with some corresponding increase on private forestland (SFig. 7). The area of low-intensity harvest (i.e., thinning) increased on public lands toward the end of the scenario (SFig. 8).

The total area burned per year tended to increase over time (SFig. 9). A large proportion of total burned area was on public forestland (89 %). Two ecoregions had distinctively high rates of fire (KM, 0.63 % year⁻¹ and IB, 0.90 % year⁻¹), whereas the CR ecoregion has almost no fire.

Pest/pathogen disturbances tended to be distributed over both public and private areas. The highest frequencies were in the EC and BM ecoregions. There was not a strong temporal pattern across the region in the area disturbed by pests/pathogens.

Carbon

Mean aboveground wood mass is particularly high in forests of the CR, WC, WV, and KM ecoregions of western Oregon and Washington (STable 1). Moderate values are found in the Northern Rocky Mountains, and lowest values in the central Idaho and western Montana. Comparison of Biome-BGC simulated mean aboveground woodmass at the ecoregion scale with means for all related FIA plots showed a good correspondence across the range of magnitude, but a tendency toward overestimates in the Biome-BGC simulations (SFig. 10).

Forest net ecosystem production (NEP), the balance of net primary production (NPP), and heterotrophic respiration (Chapin et al. 2006) were predominantly positive in the 2006–2010 period throughout the region, with maximum values in the Coast Range forests, intermediate values in the Cascade Mountains, and relatively low values in the Inland Rocky Mountain ecoregions (Fig. 3). Localized

negative NEPs were associated with low NPP and high heterotrophic respiration from harvest and fire events in recent years. There was large interannual variation in NEP, with especially low values across the region in 2003 (Fig. 4), which was the warmest year over the 1985–2010 interval (SFig. 6). In most ecoregions, there was a minor downward trend in NEP over the 25-year study period (Fig. 4).

Among nonforest cover types, farmland had the highest NEP sinks, followed by woodland and shrubland. Grasslands tended to be near carbon neutral (Fig. 3).

The net ecosystem carbon balance (NECB) in the 2006–2010 interval, i.e., the net change in carbon storage from NEP and removals in the form of direct fire emissions and harvesting of crops and wood (Chapin et al. 2006), was positive for the region (Fig. 5). At the ecoregion scale, only IB had a negative NECB in recent years and that was only on public land and was associated with high direct emissions from wildfire (SFig. 10). A higher NECB was associated with the more productive ecoregions. Slightly more carbon was sequestered on public than on private land (Fig. 5), but NECB per unit area was more positive for private forestland (47 gC m⁻² year⁻¹) than public forestland (30 gC m⁻² year⁻¹) because of large areas of public forestland in the Rocky Mountain ecoregions with low mean NEP.

Discussion

Geographic patterns

Climate provides a geographic template for the regional carbon cycle in that it strongly impacts rates of productivity, decomposition, and disturbance. In the Northwestern

Fig. 3 The distribution of net ecosystem production (mean for 2006–2010)

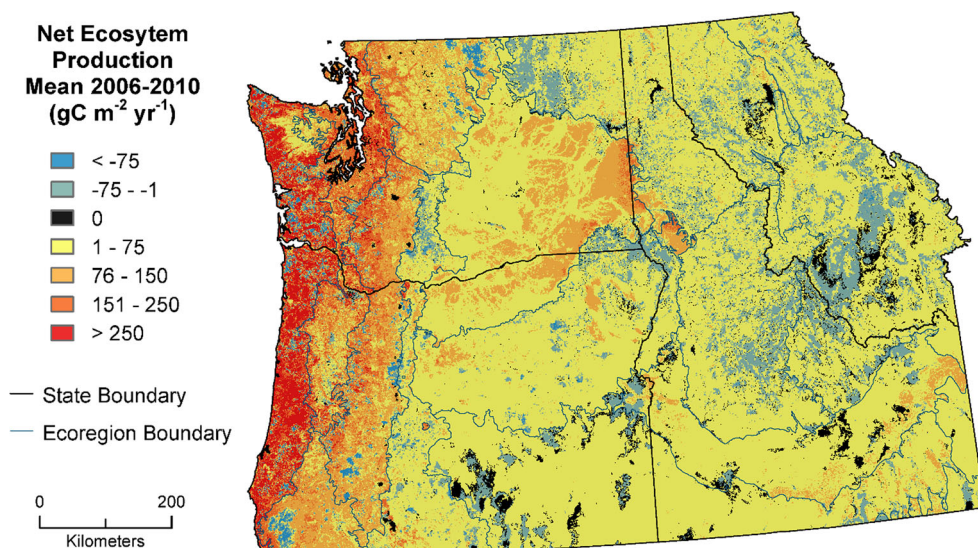


Fig. 4 Mean net ecosystem production time series by ecoregion (1986–2010)

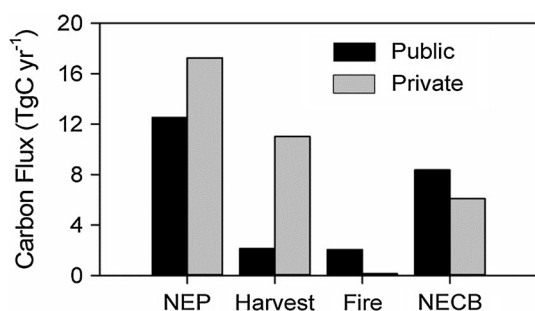
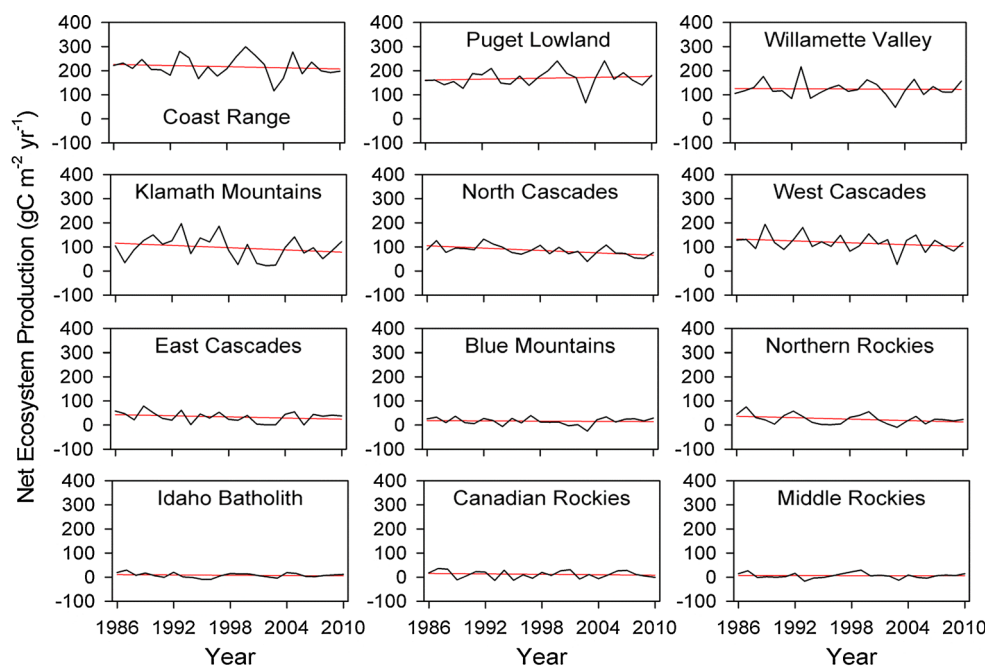


Fig. 5 Net ecosystem production, fire emissions, harvest removals, and net ecosystem carbon balance (2006–2010) for **a** private forestland, **b** public forestland

USA, the climate is primarily a function of distance from the coast and of topography (SFig. 4). High orographic precipitation and a maritime temperature regime in western Oregon and Washington are associated with the highest observed (STable 1) and potential (Latta et al. 2009) forest productivity in the region. The incidence of fire is likewise correlated with climate, with lowest values for proportional area burned along the coast, and rates increasing inland. Ecoregions have proven a useful level of stratification for examining fire/climate relationships in the Western USA (Littell et al. 2009). The incidence of pest/pathogen disturbances is similar to that of fire, with relatively low values ($<0.15\% \text{ year}^{-1}$) in western Oregon and Washington compared to the drier ecoregions to the east.

Rates of forest harvest are an overlay on the climatic template. The proportional area harvested roughly follows the distribution of forest productivity, with relatively high

rates in western Oregon and Washington. However, these rates clearly are not just productivity driven as evinced by the large policy-driven difference between rates of harvest on public and private forestland within the same ecoregion (see Fig. 2; SFig. 2).

NEP reflects both climatic influences on production/decomposition and the age class distribution of the forest, as determined by the disturbance regime. A landscape managed primarily for wood production or agriculture can have a high NEP, despite a high rate of disturbance, because harvest removals are diminishing the substrate for heterotrophic respiration (R_h). Thus, the highest mean NEPs were in the productive coastal ecoregions (SFig. 11, STable 1), which include large areas of forestland managed primarily for wood production. Cropland areas on the Columbia Plateau and the Snake River Plane have moderately high NEP. In lower productivity ecoregions, especially where fire and pest/pathogen disturbance is high, the NEP tends toward zero because of the high levels of coarse woody debris and snag carbon available for R_h . Grasslands, shrubland, and woodlands also tend to be near carbon neutral because much of NPP is available for R_h each year. Areas subject to recent stand replacing disturbances become a carbon source.

NECB is a carbon cycle metric of high interest to climate change policy makers because it represents the actual carbon sequestration on the land base (Chapin et al. 2006; Hayes and Turner 2012). The largest NECB gains were in the CR, WC, PL, and WV ecoregions (SFig. 11). These ecoregions have some of the most productive forests in the region, and mean tree biomass is rising. Carbon is also

accumulating in wood products (USDA 2011), a sink not quantified here. The ecoregions with low NECB were EC, BM, MR, IB, and CA. In these relatively dry ecoregions, NPP tends to be low and nonharvest disturbance rates are high. In Montana, the forest mortality around 2012 was over double net growth (Oswalt et al. 2014), most likely associated with a large area burned (Fig. 2), and disturbed by mountain pine beetle (Creeden et al. 2014). Ecoregions with moderate NECB gains were WC, KM, and NC.

Highest NECB levels in the NW region were found on public forestland in ecoregions of high forest productivity and low carbon removals (harvests). Fire emissions were significant on public lands in some cases in the 2006–2010 period, and in the IB ecoregion fire emissions exceeded NEP.

Temporal patterns

The overall harvest dropped in the mid-1990s, driven by a decrease in the area harvested on public lands. An increase in low-intensity harvesting on public lands toward the end of the study period reflects a growing investment in thinning as a strategy to reduce the threat of wildfire (Stephens et al. 2009). The trend of an increasing incidence of burned area in western forests that was observed here has been reported elsewhere and is associated with stronger droughts, warmer temperatures, and earlier springs (Dennison et al. 2014; Westerling et al. 2006). We did not see a temporal pattern of pest/pathogen disturbances. However, previous studies point to a link between warm summer temperatures and mountain pine beetle outbreaks (Chen and Jackson 2015) and report increases in infested area over the Western USA since 2000 (Hart et al. 2015).

The regional NEP sink was sensitive to interannual variation in climate. In 2003 (a moderate El Niño year), there was a negative NEP across all ecoregions. Eddy covariance flux towers in the region also reported record low or below average carbon sinks in 2003, with attribution focused on low precipitation and, especially, high temperatures (Thomas et al. 2009; Wharton et al. 2012). Regional carbon cycle responses to relatively warm dry years have also been reported in Europe (Reichstein et al. 2006).

The weak trend in most ecoregions toward lower NEP over the 1985–2010 interval is attributable to several factors. A trend toward warmer temperatures (Mote and Salathe 2010) and associated higher vapor pressure deficits influences photosynthesis (McDowell and Allen 2015). In both observations (Meinzer 1982) and our simulations, high VPDs have a negative impact on stomatal conductance and hence gross primary production. A second contributing factor is the trend toward older stand ages on public lands; low harvest levels have contributed to an

increase in mean stand age in many areas. Generally, NEP peaks around a stand age of about 50 because NPP is near maximum (Turner and Long 1975) and R_h is relatively low (many of the residues from the stand-initiating disturbance have been respired). In relatively older stands, NPP comes down (Gower et al. 1996) and R_h increases because of increased inputs to the dead wood pool from mortality.

The effect of decreasing NEP and increasing direct fire emissions is a decline in regional NECB across the study period. Climate projections in the Northwest US call for warmer temperatures, with wetter winters but possibly drier summers (Mote and Salathe 2010). Given the observed relationships of area burned to summer temperature and precipitation (Littell et al. 2009), regional fire emissions will likely continue to increase (Rogers et al. 2011; Turner et al. 2015b). Rates of pest/pathogen outbreaks may likewise increase. Future rates of harvest on private lands will be potentially constrained in western Oregon if projected climate change driven fires cover large areas (Turner et al. 2015b).

Possible ameliorating factors in the regional carbon budget of the future are beneficial CO₂ effects on photosynthesis and water use efficiency (Keenan et al. 2013), and increased productivity at high elevations (Latta et al. 2010). The complexity of the multiple influences on the regional carbon budget support development of regional scenarios based on landscape simulation models that account for changing disturbance regimes and ecophysiology-based influences on ecosystem carbon cycle dynamics.

Modeling limitations

Uncertainty in our simulated carbon stocks and flux estimates arises from errors in the spatially distributed inputs to the model, as well as from Biome-BGC model structure and parameter uncertainty. Uncertainties have previously been investigated in the distributed meteorological data (e.g., Hasenauer et al. 2003; Oyler et al. 2015), soil depth and texture (Peterman et al. 2014), disturbance mapping (Cohen et al. 2010), and stand age mapping (Ohmann and Gregory 2002). Observations of Biome-BGC parameters were compiled by (White et al. 2000), and there is obvious species-level variation within a plant functional type. In our Biome-BGC modeling, we addressed this issue by use of ecoregion-level parametrization based on (1) observations (e.g., foliar nitrogen concentration) and (2) parameter optimization (with reference to FIA observations). In Law et al. (2006), we further discuss our use of eddy covariance flux tower observations, FIA data, ecological field plot measurements, and associated Monte Carlo analyses, to characterize multiple aspects of Biome-BGC model uncertainty.

Efforts at validation of carbon stocks include comparison to aggregated FIA plot data. The comparison here (SFig. 10) of ecoregion mean values suggests a positive bias in the simulated tree carbon stocks. The explanation may lie in a difference in the age class distributions in the wall-to-wall simulations versus the sample of FIA plots (Duane et al. 2010). Alternate biomass mapping approaches, especially individual tree-level analyses based on airborne lidar (Duncanson et al. 2015), are beginning to offer improved possibilities for more direct validation of biomass estimates.

Regional carbon fluxes can also be evaluated, by way of inversion modeling (Turner et al. 2011b) in which observations of spatial and temporal patterns in atmospheric CO₂ concentration are used to infer a flux. However, the number of CO₂ observations in the Pacific Northwest is limited, and uncertainties in the inversion results remain large (Gockede et al. 2010). Comprehensive satellite-based observations of atmospheric CO₂ concentration (OCO-2 2015) are beginning to be used in inversion analyses and will improve inversion accuracy over time, thus providing an independent check on bottom-up simulation of regional fluxes.

Conclusions

Spatial and temporal heterogeneity in climate and ecosystem disturbance regimes have strong effects on the carbon cycle and make it challenging to monitor and evaluate regional carbon stocks and flux. Application of a spatially distributed carbon cycle process model, which integrates observations from meteorological stations, satellite-borne sensors, and forest inventory plots, is a viable approach to addressing this challenge. In the Northwest US, a strong west-to-east environmental climate gradient strongly regulates spatial patterns in vegetation productivity, organic matter decomposition, and forest disturbances. Coastal and West Cascade mountain ecozones have high NEPs, which are balanced to some degree by high levels of harvest removals (largely on private forestland). These ecozones are significant carbon sinks. The ecozones to the east have lower NEPs and higher levels of fire and pest/pathogen disturbances, hence low rates of carbon sequestration. Interannual variation in climate influences both NEP and fire emissions, and in relatively warm years (e.g., 2003), the region as a whole can become a carbon source. Limited opportunities for evaluating regional carbon cycle simulations based on process models exist in the form of aggregated forest inventory observations and atmospheric inversion analyses. Improvements in remote sensing-based observations, including airborne lidar for tree biomass and satellite-borne spectrometers for atmospheric CO₂

concentration, are expanding the options for validation of simulated carbon fluxes.

Acknowledgments Support was provided by the NASA Terrestrial Ecology Program (NNX12AK59G). Landsat data from US Geological Survey Eros Data Center, Daymet climate data from the North American Carbon Program (served from the Oak Ridge National Laboratory Biogeochemical Dynamics Distributed Active Archive Center), and plot data from the USDA Forest Service Forest Inventory and Analysis Program were essential to this study.

References

- Abatzoglou JT, Rupp DE, Mote PW (2014) Seasonal climate variability and change in the Pacific Northwest of the United States. *J Clim* 27:2125–2142. doi:10.1175/jcli-d-13-00218.1
- Baldocchi D, Falge E, Gu LH, Olson R, Hollinger D, Running S, Anthoni P, Bernhofer C, Davis K, Evans R, Fuentes J, Goldstein A, Katul G, Law B, Lee XH, Malhi Y, Meyers T, Munger W, Oechel W, KTP U, Pilegaard K, Schmid HP, Valentini R, Verma S, Vesala T, Wilson K, Wofsy S (2001) FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull Am Meteorol Soc* 82:2415–2434. doi:10.1175/1520-0477(2001)082<2415:fantts>2.3.co;2
- Barnett TP, Pierce DW, Hidalgo HG, Bonfils C, Santer BD, Das T, Bala G, Wood AW, Nozawa T, Mirin AA, Cayan DR, Dettinger MD (2008) Human-induced changes in the hydrology of the western United States. *Science* 319:1080–1083. doi:10.1126/science.1152538
- Beedlow PA, Lee EH, Tingey DT, Waschmann RS, Burdick CA (2013) The importance of seasonal temperature and moisture patterns on growth of Douglas-fir in western Oregon, USA. *Agr For Meteorol* 169:174–185. doi:10.1016/j.agrformet.2012.10.010
- Campbell J, Donato D, Azuma DL, Law B (2007) Pyrogenic carbon emission from a large wildfire in Oregon, United States. *J Geophys Res Biogeosci* 12:G04014. doi:10.1029/2007JG000451
- Chapin FS, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, Baldocchi DD, Clark DA, Harmon ME, Schimel DS, Valentini R, Wirth C, Aber JD, Cole JJ, Goulden ML, Harden JW, Heimann M, Howarth RW, Matson PA, McGuire AD, Melillo JM, Mooney HA, Neff JC, Houghton RA, Pace ML, Ryan MG, Running SW, Sala OE, Schlesinger WH, Schulze ED (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9:1041–1050. doi:10.1007/s10021-005-0105-7
- Chen HP, Jackson PL (2015) Spatiotemporal mapping of potential mountain pine beetle emergence—Is a heating cycle a valid surrogate for potential beetle emergence? *Agr For Meteorol* 206:124–136. doi:10.1016/j.agrformet.2015.03.006
- Cohen WB, Yang ZG, Kennedy R (2010) Detecting trends in forest disturbance and recovery using yearly Landsat time series: 2. TimeSync—tools for calibration and validation. *Remote Sens Environ* 114:2911–2924. doi:10.1016/j.rse.2010.07.010
- CONUS (2007) Conterminous United States multi-layer soil characteristics data set for regional climate and hydrology modeling. http://www.soilinfo.psu.edu/index.cgi?soil_data&conus. Accessed 10 Aug 2015
- Creeden EP, Hicke JA, Buotte PC (2014) Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *For Ecol Manag* 312:239–251. doi:10.1016/j.foreco.2013.09.051

- Curtis PS, Hanson PJ, Barford P, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agr For Meteorol* 113:3–19. doi:[10.1016/s0168-1923\(02\)00099-0](https://doi.org/10.1016/s0168-1923(02)00099-0)
- Dennison PE, Brewer SC, Arnold JD, Moritz MA (2014) Large wildfire trends in the western United States, 1984–2011. *Geophys Res Lett* 41:2928–2933. doi:[10.1002/2014gl059576](https://doi.org/10.1002/2014gl059576)
- Duane MV, Cohen WB, Campbell JL, Hudiburg T, Weyeremann D, Turner DP (2010) Implications of two different field-sampling designs on Landsat-based forest age maps used to model carbon in Oregon forests. *For Sci* 65:405–416
- Duncanson LI, Dubayah RO, Rosette J, Parker G (2015) The importance of spatial detail: assessing the utility of individual crown information and scaling approaches for lidar-based biomass density estimation. *Remote Sens Environ* 168:102–112. doi:[10.1016/j.rse.2015.06.021](https://doi.org/10.1016/j.rse.2015.06.021)
- GAP (2014) US Geological Survey, Gap Analysis Program (GAP). National Land Cover, Version 2. <http://gapanalysis.usgs.gov/gaplandcover/data/>. Accessed 10 Aug 2015
- Garman SL, Swanson FJ, Spies TA (1999) Past, present, future landscape patterns in the Douglas-fir region of the Pacific Northwest. In: Rochelle JA, Lehmann LA, Wisniewski J (eds) *Forest fragmentation: wildlife and management implications*. Brill academic publishing, The Netherlands, pp 61–86
- GCP (2015) Global Carbon Project. <http://www.globalcarbonproject.org/carbonbudget/index.htm>. Accessed 10 Aug 2015
- Gockede M, Turner DP, Michalak AM, Vickers D, Law BE (2010) Sensitivity of a subregional scale atmospheric inverse CO₂ modeling framework to boundary conditions. *J Geophys Res Atmos* 115:15. doi:[10.1029/2010jd014443](https://doi.org/10.1029/2010jd014443)
- Gonzalez P, Battles JJ, Collins BM, Robards T, Saah DS (2015) Aboveground live carbon stock changes of California wildland ecosystems, 2001–2010. *For Ecol Manag* 348:68–77. doi:[10.1016/j.foreco.2015.03.040](https://doi.org/10.1016/j.foreco.2015.03.040)
- Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. *Trends Ecol Evol* 11:378–382. doi:[10.1016/0169-5347\(96\)10042-2](https://doi.org/10.1016/0169-5347(96)10042-2)
- Gray AN, Whittier TR (2014) Carbon stocks and changes on Pacific Northwest national forests and the role of disturbance, management, and growth. *For Ecol Manag* 328:167–178. doi:[10.1016/j.foreco.2014.05.015](https://doi.org/10.1016/j.foreco.2014.05.015)
- Hasenauer H, Merganicova K, Petritsch R, Pietsch SA, Thornton PE (2003) Validating daily climate interpolations over complex terrain in Austria. *Agr For Meteorol* 119:87–107. doi:[10.1016/0169-5347\(96\)10042-2](https://doi.org/10.1016/0169-5347(96)10042-2)
- Hart SJ, Schoennagel T, Veblen TT, Chapman TB (2015) Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proc Natl Acad Sci USA* 112:4375–4380. doi:[10.1073/pnas.1424037112](https://doi.org/10.1073/pnas.1424037112)
- Hayes DJ, Turner DP (2012) The need for “apples-to-apples” comparisons of carbon dioxide source and sink estimates. *EOS* 93:404–405
- Hibbard KA, Law BE, Reichstein M, Sulzman J (2005) An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry* 73:29–70. doi:[10.1007/s10533-004-2946-0](https://doi.org/10.1007/s10533-004-2946-0)
- Hicke JA, Meddens AJH, Allen CD, Kolden CA (2013) Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environ Res Lett* 8:8. doi:[10.1088/1748-9326/8/3/035032](https://doi.org/10.1088/1748-9326/8/3/035032)
- Johnstone JA, Mantua NJ (2014) Atmospheric controls on northeast Pacific temperature variability and change, 1900–2012. *Proc Natl Acad Sci USA* 111:14360–14365. doi:[10.1073/pnas.1318371111](https://doi.org/10.1073/pnas.1318371111)
- Keenan TF, Hollinger DY, Bohrer G, Dragoni D, Munger JW, Schmid HP, Richardson AD (2013) Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499:324. doi:[10.1038/nature12291](https://doi.org/10.1038/nature12291)
- Kennedy RE, Yang ZG, Cohen WB (2010) Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr—temporal segmentation algorithms. *Remote Sens Environ* 114:2897–2910. doi:[10.1016/j.rse.2010.07.008](https://doi.org/10.1016/j.rse.2010.07.008)
- Kennedy RE, Yang ZQ, Cohen WB, Pfaff E, Braaten J, Nelson P (2012) Spatial and temporal patterns of forest disturbance and regrowth within the area of the Northwest Forest Plan. *Remote Sens Environ* 122:117–133. doi:[10.1016/j.rse.2011.09.024](https://doi.org/10.1016/j.rse.2011.09.024)
- Latta G, Temesgen H, Adams D, Barrett T (2010) Analysis of potential impacts of climate change on forests of the United States Pacific Northwest. *Forest Ecol Manag* 259:720–729. doi:[10.1016/0169-5347\(96\)10042-2](https://doi.org/10.1016/0169-5347(96)10042-2)
- Law BE et al (2006) Carbon fluxes across regions: observational constraints at multiple scales. In: Wu J, Jones B, Li H, Loucks O (eds) *Scaling and uncertainty analysis in ecology: methods and applications*. Columbia university press, New York, pp 167–190
- Latta G, Temesgen H, Barrett TM (2009) Mapping and imputing potential productivity of Pacific Northwest forests using climate variables. *Can J For Res* 39:1197–1207. doi:[10.1139/x09-046](https://doi.org/10.1139/x09-046)
- Law BE, Turner D, Campbell J, Van Tuyl S, Ritts WD, Cohen WB (2004) Disturbance and climate effects on carbon stocks and fluxes across Western Oregon USA. *Global Change Biol* 10:1429–1444. doi:[10.1111/j.1365-2486.2004.00822.x](https://doi.org/10.1111/j.1365-2486.2004.00822.x)
- Law BE, Waring RH (2015) Carbon implications of current and future effects of drought, fire and management on Pacific Northwest forests. *For Ecol Manag* 355:4–14. doi:[10.1016/j.foreco.2014.11.023](https://doi.org/10.1016/j.foreco.2014.11.023)
- Le Quere C, Moriarty R, Andrew RM, Peters GP, Ciais P, Friedlingstein P, Jones SD, Sitch S, Tans P, Arneeth A, Boden TA, Bopp L, Bozec Y, Canadell JG, Chini LP, Chevallier F, Cosca CE, Harris I, Hoppema M, Houghton RA, House JI, Jain AK, Johannessen T, Kato E, Keeling RF, Kitidis V, Goldewijk KK, Koven C, Landa CS, Landschutzer P, Lenton A, Lima ID, Marland G, Mathis JT, Metzl N, Njiri Y, Olsen A, Ono T, Peng S, Peters W, Pfeil B, Poulter B, Raupach MR, Regnier P, Rodenbeck C, Saito S, Salisbury JE, Schuster U, Schwinger J, Seferian R, Segsneider J, Steinhoff T, Stocker BD, Sutton AJ, Takahashi T, Tilbrook B, van der Werf GR, Viovy N, Wang YP, Wanninkhof R, Wiltshire A, Zeng N (2014) Global carbon budget 2014. *Earth Syst Sci Data* 7:47–85. doi:[10.5194/essd-7-47-2015](https://doi.org/10.5194/essd-7-47-2015)
- Littell JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire area burned in western U.S. ecoregions, 1916–2003. *Ecol Appl* 19:1003–1021. doi:[10.1890/07-1183.1](https://doi.org/10.1890/07-1183.1)
- Liu JX et al (2011) Estimating California ecosystem carbon change using process model and land cover disturbance data: 1951–2000. *Ecol Model* 222:2333–2341. doi:[10.1016/j.ecolmodel.2011.03.042](https://doi.org/10.1016/j.ecolmodel.2011.03.042)
- Lu XL et al (2013) A contemporary carbon balance for the Northeast Region of the United States. *Environ Sci Technol* 47:13230–13238. doi:[10.1021/es403097z](https://doi.org/10.1021/es403097z)
- McDowell NG, Allen CD (2015) Darcy’s law predicts widespread forest mortality under climate warming. *Nat Clim Change* 5:669–672. doi:[10.1038/nclimate2641](https://doi.org/10.1038/nclimate2641)
- Meigs GW, Kennedy RE, Gray AN, Gregory MJ (2015) Spatiotemporal dynamics of recent mountain pine beetle and western spruce budworm outbreaks across the Pacific Northwest region, USA. *Remote Sens Environ* 339:71–86. doi:[10.1016/j.foreco.2014.11.030](https://doi.org/10.1016/j.foreco.2014.11.030)
- Meigs GW, Turner DP, Ritts WD, Yang ZQ, Law BE (2011) Landscape-scale simulation of heterogeneous fire effects on pyrogenic carbon emissions, tree mortality, and net ecosystem production. *Ecosystems* 14:758–775. doi:[10.1007/s10021-011-9444-8](https://doi.org/10.1007/s10021-011-9444-8)

- Meinzer FC (1982) The effect of vapor pressure on stomatal control of gas exchange in Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Oecologia* 54:236–242. doi:[10.1007/bf00378398](https://doi.org/10.1007/bf00378398)
- Mote PW (2003) Trends in temperature and precipitation in the Pacific Northwest during the twentieth century. *Northwest Sci* 77:271–282
- Mote PW (2006) Climate-driven variability and trends in mountain snowpack in western North America. *J Clim* 19:6209–6220. doi:[10.1175/jcli3971.1](https://doi.org/10.1175/jcli3971.1)
- Mote PW, Salathe EP (2010) Future climate in the Pacific Northwest. *Clim Change* 102:29–50. doi:[10.1007/s10584-010-9848-z](https://doi.org/10.1007/s10584-010-9848-z)
- MTBS (2015) Monitoring Trends in Burn Severity. <http://www.mtbs.gov/>. Accessed 10 Aug 2015
- NLCD (2006) National land cover data. <http://www.epa.gov/mlrc/nlcd.html>. Accessed 10 Aug 2015
- OCO-2 (2015) Orbiting Carbon Observatory-2. <http://oco.jpl.nasa.gov/>. Accessed 10 Aug 2015
- Ohmann JL, Gregory MJ (2002) Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. *Can J For Res* 32:725–741. doi:[10.1139/x02-011](https://doi.org/10.1139/x02-011)
- Omernik JM (1987) Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Ann Assoc Am Geogr* 77:118–125. doi:<http://www.epa.gov/wed/pages/ecoregions/ecoregions.htm>. Accessed 10 Aug 2015
- ORNL (2014) Oak Ridge National Laboratory. http://daac.ornl.gov/DAYMET/guides/Daymet_mosaics.html#Daymet_m_citation. Accessed 10 Aug 2015
- Oswalt SN, Smith WB, Miles PD, Pugh SA (2014) Forest Resources of the United States, 2012: a technical document supporting the forest Service 2015 update of the RPA Assessment. General Technical Report WO-91. U.S. Department of Agriculture, Forest Service
- Oyler JW, Dobrowski SZ, Ballantyne AP, Klene AE, Running SW (2015) Artificial amplification of warming trends across the mountains of the western United States. *Geophys Res Lett* 42:153–161. doi:[10.1002/2014gl062803](https://doi.org/10.1002/2014gl062803)
- Pederson GT, Graumlich LJ, Fagre DB, Kipfer T, Muhlfield CC (2010) A century of climate and ecosystem change in Western Montana: what do temperature trends portend? *Clim Change* 98:133–154
- Peterman W, Bachelet D, Ferschweiler K, Sheehan T (2014) Soil depth affects simulated carbon and water in the MC2 dynamic global vegetation model. *Ecol Model* 294:84–93. doi:[10.1016/j.ecolmodel.2014.09.025](https://doi.org/10.1016/j.ecolmodel.2014.09.025)
- Preisler HK, Hicke JA, Ager AA, Hayes JL (2012) Climate and weather influences on spatial temporal patterns of mountain pine beetle populations in Washington and Oregon. *Ecology* 93:2421–2434
- Reichstein M, Ciais P, Papale D, Valentini R, Running S, Viovy N, Cramer W, Granier A, Ogee J, Allard V, Aubinet M, Bernhofer C, Buchmann N, Carrara A, Grunwald T, Heimann M, Heinesch B, Knohl A, Kutsch W, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Pilegaard K, Pumpanen J, Rambal S, Schaphoff S, Seufert G, Soussana JF, Sanz MJ, Vesala T, Zhao M (2006) Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. *Global Change Biol* 12:1–18. doi:[10.1111/j.1365-2486.2006.01224.x](https://doi.org/10.1111/j.1365-2486.2006.01224.x)
- Rogers BM, Neilson RP, Drapek R, Lenihan JM, Wells JR, Bachelet D, Law BE (2011) Impacts of climate change on fire regimes and carbon stocks of the U.S. Pacific Northwest. *J Geophys Res Biogeosci* 116:13. doi:[10.1029/2011jg001695](https://doi.org/10.1029/2011jg001695)
- Schwalm CR, Williams CA, Schaefer K, Baldocchi D, Black TA, Goldstein AH, Law BE, Oechel WC, Kyaw TPU, Scott RL (2012) Reduction in carbon uptake during turn of the century drought in western North America. *Nat Geosci* 5:551–556. doi:[10.1038/ngeo1529](https://doi.org/10.1038/ngeo1529)
- Soule PT, Knapp PA (2013) Radial growth rates of two co-occurring coniferous trees in the Northern Rockies during the past century. *J Arid Environ* 94:87–95. doi:[10.1016/j.jaridenv.2013.02.005](https://doi.org/10.1016/j.jaridenv.2013.02.005)
- Stephens SL, Moghaddas JJ, Edminster C, Fiedler CE, Haase S, Harrington M, Keeley JE, Knapp EE, McIver JD, Metlen K, Skinner CN, Youngblood A (2009) Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. *Ecol Appl* 19:305–320. doi:[10.1890/07-1755.1](https://doi.org/10.1890/07-1755.1)
- Thomas CK, Law BE, Irvine J, Martin JG, Pettijohn JC, Davis KJ (2009) Seasonal hydrology explains interannual and seasonal variation in carbon and water exchange in a semiarid mature ponderosa pine forest in central Oregon. *J Geophys Res Biogeosci* 114:22. doi:[10.1029/2009jg001010](https://doi.org/10.1029/2009jg001010)
- Thomas JW, Franklin JF, Gordon J, Johnson KN (2006) The northwest forest plan: origins, components, implementation experience, and suggestions for change. *Conserv Biol* 20:277–287. doi:[10.1111/j.1523-1739.2006.00385.x](https://doi.org/10.1111/j.1523-1739.2006.00385.x)
- Thornton PE, Law BE, Gholz HL, Clark KL, Falge E, Ellsworth DS, Golstein AH, Monson RK, Hollinger D, Falk M, Chen J, Sparks JP (2002) Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agr For Meteorol* 113:185–222. doi:[10.1111/j.1523-1739.2006.00385.x](https://doi.org/10.1111/j.1523-1739.2006.00385.x)
- Thornton PE, Thornton MM, Mayer BW, Wilhelmi Y, Wei Y, Devarakonda R, Cook RB (2014) Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 2. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA. Available: <http://daac.ornl.gov>
- Thornton PE, Running SW, White MA (1997) Generating surfaces of daily meteorological variables over large regions of complex terrain. *J Hydrol* 190:214–251. doi:[10.1016/s0022-1694\(96\)03128-9](https://doi.org/10.1016/s0022-1694(96)03128-9)
- Turner DP, Ritts D, Kennedy RE, Gray A, Yang Z (2015a) Effects of harvest, fire, and pest/pathogen disturbances on the West Cascades ecoregion carbon balance. *Carbon Balance Manag* 10:12. doi:[10.1186/s13021-015-0022-9](https://doi.org/10.1186/s13021-015-0022-9)
- Turner DP, Conklin DR, Bolte JP (2015b) Projected climate change impacts on forest land cover and land use over the Willamette River Basin, Oregon, USA. *Clim Change* 133:335–348. doi:[10.1007/s10584-015-1465-4](https://doi.org/10.1007/s10584-015-1465-4)
- Turner DP, Ritts WD, Yang ZQ, Kennedy RE, Cohen WB, Duane MV, Thornton PE, Law BE (2011a) Decadal trends in net ecosystem production and net ecosystem carbon balance for a regional socioecological system. *For Ecol Manag* 262:1318–1325. doi:[10.1007/s10584-015-1465-4](https://doi.org/10.1007/s10584-015-1465-4)
- Turner DP, Gockede M, Law BE, Ritts WD, Cohen WB, Yang Z, Hudiburg T, Kennedy R, Duane M (2011b) Multiple constraint analysis of regional land-surface carbon flux. *Tellus* 63B:207–221. doi:[10.1111/j.1600-0889.2011.00525.x](https://doi.org/10.1111/j.1600-0889.2011.00525.x)
- Turner DP, Ritts WD, Law BE, Cohen WB, Yang Z, Hudiburg T, Campbell JL, Duane M (2007) Scaling net ecosystem production and net biome production over a heterogeneous region in the western United States. *Biogeosciences* 4:597–612
- Turner J, Long JN (1975) Accumulation of organic matter in a series of Douglas-fir stands. *Can J For Res* 5:681–690
- Turner DP, Ollinger SV, Kimball JS (2004) Integrating remote sensing and ecosystem process models for landscape to regional scale analysis of the carbon cycle. *Bioscience* 54:573–584. doi:[10.1641/0006-3568\(2004\)054\[0573:irsaepl\]2.0.co;2](https://doi.org/10.1641/0006-3568(2004)054[0573:irsaepl]2.0.co;2)
- USDA (2011) U.S. Agriculture and Forestry Greenhouse Gas Inventory: 1990–2008. Technical Bulletin No. 1930
- USGS (2015) Omernik Level 3 Ecoregions for the U.S. (including Alaska) for Use as a Reference Data Collection. <https://www>

- sciencebase.gov/catalog/folder/55c77f7be4b08400b1fd82d4?offset=60&max=30
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT (2009) Widespread increase of tree mortality rates in the Western United States. *Science* 323:521–524. doi:[10.1126/science.1165000](https://doi.org/10.1126/science.1165000)
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increases western U.S. forest wildfire activity. *Science* 313:940–943. doi:[10.1126/science.1128834](https://doi.org/10.1126/science.1128834)
- Wharton S, Falk M, Bible K, Schroeder M, Paw KT (2012) Old-growth CO₂ flux measurements reveal high sensitivity to climate anomalies across seasonal, annual and decadal time scales. *Agr For Meteorol* 161:1–14. doi:[10.1016/j.agrformet.2012.03.007](https://doi.org/10.1016/j.agrformet.2012.03.007)
- White MA, Thornton PE, Running SW, Nemani RR (2000) Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. *Earth Interact* 4:1–85
- Woudenberg SW, Conkling BL, O'Connell BM, LaPoint EB, Turner JA, Waddell KL (2010) The Forest Inventory and Analysis database: description and user manual version 4.0 for Phase 2, USDA Forest Service, General Technical Report RMRS-GTR-245, USDA Forest Service, General Technical Report RMRS-GTR-245