# Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States

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*Citation:* Buotte, P. C., B. E. Law, W. J. Ripple, and L. T. Berner. 2019. Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. Ecological Applications 00(00):e02039. 10.1002/eap.2039

Abstract. Forest carbon sequestration via forest preservation can be a viable climate change mitigation strategy. Here, we identify forests in the western conterminous United States with high potential carbon sequestration and low vulnerability to future drought and fire, as simulated using the Community Land Model and two high carbon emission scenario (RCP 8.5) climate models. High-productivity, low-vulnerability forests have the potential to sequester up to 5,450 Tg CO<sub>2</sub> equivalent (1,485 Tg C) by 2099, which is up to 20% of the global mitigation potential previously identified for all temperate and boreal forests, or up to ~6 yr of current regional fossil fuel emissions. Additionally, these forests currently have high above- and belowground carbon density, high tree species richness, and a high proportion of critical habitat for endangered vertebrate species, indicating a strong potential to support biodiversity into the future and promote ecosystem resilience to climate change. We stress that some forest lands have low carbon sequestration potential but high biodiversity, underscoring the need to consider multiple criteria when designing a land preservation portfolio. Our work demonstrates how process models and ecological criteria can be used to prioritize landscape preservation for mitigating greenhouse gas emissions and preserving biodiversity in a rapidly changing climate.

*Key words: biodiversity; carbon sequestration; climate change; Community Land Model (CLM); forest; mitigation; process modeling; western United States.* 

## INTRODUCTION

Since the signing of the United Nations Framework Convention on Climate Change in Rio de Janeiro in 1992, the United Nations has recognized the need to formulate a global response to increasing greenhouse gas concentrations in our atmosphere. The subsequent adoptions of the Sustainable Development Goals (United Nations General Assembly 2015) and the Paris Agreement (United Nations Framework Convention on Climate Change (UNFCC) 2015) provided global targets for preserving biodiversity and limiting the negative effects of increasing greenhouse gas concentrations. Limiting global temperature to 1.5°C above the preindustrial average would limit negative climate impacts (IPCC 2018), including negative effects on biodiversity (Smith et al. 2018). Unfortunately, substantial enhancement or over-delivery of emissions goals in the Paris Agreement is necessary to limit warming to less than 2°C (Rogelj et al. 2016). Missing this target could destabilize Earth's climate, terrestrial, and aquatic systems (Steffen et al. 2018) with catastrophic consequences for biodiversity (Davis et al. 2018), ecosystem services, and

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humans (Barnosky et al. 2012). Already, ample observational evidence exists that changes in climate are inducing ecosystem transformations through tree mortality (Allen et al. 2010, Millar and Stephenson 2015) and changes in species composition (Allen and Breshears 1998, Millar and Stephenson 2015). Process-based (Settele et al. 2014, McDowell et al. 2016) and statistical (Rehfeldt et al. 2006, Williams et al. 2007, Pearson et al. 2013) models indicate a strong potential for continued ecological transformation, and paleological analyses indicate that, if we continue on our current emission trajectory, drastic changes in global ecosystem structure and function are likely by the end of this century (Nolan et al. 2018*a*).

Along with emissions, multiple biogeophysical processes, including carbon uptake by the land and oceans and ocean heat exchange (Solomon et al. 2009), influence atmospheric CO<sub>2</sub> (Canadell et al. 2007, Le Quere et al. 2018) and the integrated Earth system trajectory (Barnosky et al. 2012, Steffen et al. 2018). Recent measurements indicate the ocean heat uptake is at the high end of previous estimates (Resplandy et al. 2018), and decreasing land carbon uptake relative to carbon emissions (Canadell et al. 2007) is contributing to increasing atmospheric CO<sub>2</sub> and chances of climate destabilization (Barnosky et al. 2012, Steffen et al. 2018). Land preservation and timber harvest management (natural climate

Manuscript received 4 March 2019; revised 10 October 2019; accepted 21 October 2019. Corresponding Editor: Yude Pan.

solutions) are viable options for avoiding greenhouse gas emissions and increasing the magnitude of the land carbon sink (Griscom et al. 2017).

Forest management (e.g., land preservation, reduced harvest) can contribute to climate change mitigation and the preservation of biodiversity (MEA 2005). Globally, improvements to land management could provide an estimated 37% of the mitigation needed to stabilize warming below 2°C by 2039 (Griscom et al. 2017). Land management can also mitigate the negative effects that climate-induced ecosystem transformations have on bio-diversity and watersheds, which influence ecosystem services that contribute to human well-being (Canadell and Raupach 2008, Griscom et al. 2017). The effects of land-use change vary globally (Bright et al. 2017), therefore regional analyses (Cameron et al. 2017, Law et al. 2018) are ideal for prioritizing lands for preservation and improving harvest management.

Here, we simulate potential forest carbon sequestration in the western United States, prioritize forest lands for preservation (i.e., no harvest) based on potential carbon sequestration and vulnerability to drought or fire, and compare this carbon priority ranking with measures of biodiversity to illustrate the spatial synergies and incongruities between these two preservation metrics. We use the Community Land Model 4.5 (CLM) to simulate future forest productivity and vulnerability to drought and fire. We prioritize land based on the spatial convergence of low future vulnerability to natural disturbance and three levels of potential productivity and determine the CO<sub>2</sub> mitigation potential that preserving medium- and high-priority forests could provide. We show the co-benefits and trade-offs to biodiversity preservation and ecosystem resilience by comparing current observations of aboveground carbon (Wilson et al. 2013), soil carbon (Weider et al. 2014), and species richness (Jenkins et al. 2015, USGS National Gap Analysis Program 2018) across the three forest carbon preservation priority categories. We use these combined analyses to underscore the need to consider multiple criteria when selecting forest lands for preservation.

# MATERIALS AND METHODS

# Simulations of future forest vulnerability and potential carbon sequestration

We used the Community Land Model, version 4.5 (CLM; Oleson et al. 2013) to simulate the forest carbon cycle across the western United States (Appendix S1: Fig. S1) at a  $4 \times 4$  km spatial resolution. The CLM is the land surface model within the Community Earth System Model (Hurrell et al. 2013). The CLM has prognostic carbon and nitrogen cycles and calculates multiple biogeochemical and biophysical process, such as photosynthesis, autotrophic and heterotrophic respiration, carbon allocation to plant tissues, decomposition, and surface energy balance. It also has a fire module that

predicts area burned under future climate and biomass fuel conditions. Here, we used climate projections, described below, prescribed vegetation type (Appendix S1: Fig. S1), and prescribed soil type to drive the model. We employed several modifications that improved the CLM's simulation of aboveground carbon, net primary productivity, and ecosystem respiration across the western United States (Buotte et al. 2019b). In particular, these include specification of physiological parameters controlling photosynthesis for the dominant species in the major forest types (Appendix S1: Fig. S1) of the western United States (Berner and Law 2016, Law et al. 2018, Buotte et al. 2019b), enhanced drought sensitivity through species-specific stomatal response to soil moisture and leaf shedding during periods of drought stress (Buotte et al. 2019b), and improved fire simulation by incorporating regional ignition probabilities and fuel load constraints (Buotte et al. 2019b).

The CLM was started from bare ground and run with 1901–1920 climate data and prognostic fire turned off until soil carbon pools reached equilibrium. Improvements to the representation of drought stress and prognostic fire were implemented beginning in 1901. From 1901 to 1978, we forced CLM with CRUNCEP climate data (Mitchell and Jones 2005) statistically downscaled to  $4 \times 4$  km and bias-corrected to our 1979–2014 climate data. Climate data from 1979 to 2014 were disaggregated from daily to 3-h intervals at  $4 \times 4$  km resolution (Abatzoglou 2013). Downscaling and disaggregation details are provided in Buotte et al. (2019b). Furthermore, we used prescribed harvest to insure the model represented present-day stand ages (Pan et al. 2011).

It is crucial to assess model performance and thus we previously evaluated the modeled present-day carbon stocks, carbon fluxes, and burned area through comparisons with a suite of field and satellite observations (Buotte et al. 2019a,b). In particular, we compared modeled carbon stocks and fluxes with aboveground biomass interpolated from plot inventories (Wilson et al. 2013), carbon fluxes from five AmeriFlux sites, fluxes derived from plot inventories in Washington, Oregon, and California (Hudiburg et al. 2009, 2011), and net primary productivity estimated from the MODIS satellites (Berner et al. 2017a). We also compared modeled burned area with a burned area data set derived from the Landsat satellites (Eldenshenk et al. 2007). As detailed in Buotte et al. (2019b), simulated carbon fluxes agreed well with a variety of observations. Simulated net primary productivity was within the range of observed and satellite-derived net primary productivity at the state level. Across all forests in the western United States, simulated aboveground carbon was within one standard deviation of observation-based aboveground carbon (observed mean = 30.5 Mg C/ha, SD = 39.7 Mg C/ha, CLM mean = 59.1 Mg C/ha, SD = 45.5 Mg C/h,  $R^2 = 0.80$ ). When grouped by forest type, simulated aboveground carbon was highly correlated with

observations with a tendency toward higher simulated values ( $R^2 = 0.84$ , mean bias error = 4%). Over the forested domain, simulated area burned was highly correlated with observed area burned ( $R^2 = 0.75$ ), with a 28.6% overestimate when compared with observations from the Monitoring Trends in Burn Severity (MTBS) database over 1984–2012 (Eldenshenk et al. 2007). However, Whittier and Gray (2016) determined that MTBS underestimates burn area by 20% when compared with inventory data, which implies CLM overestimates may be as low as 8%. These assessments illustrate that the model is accurately simulating important aspects of the current regional forest carbon cycle.

Our future CLM simulations were driven with two future climate projections. We used a Representative Concentration Pathway (RCP) 8.5 carbon dioxide emissions scenario for our future simulations because it best represents our current trajectory (Peters et al. 2013). We chose general circulation models (GCMs) based on data availability, representation of historical climate, and coverage of the range of projected future climate (Buotte et al. 2019b). We selected IPSL-CM5A-MR, which projects warm and dry future conditions, and MIROC5, which is close to the multi-model average for future temperature and precipitation across the western United States (Buotte et al. 2019b). Climate projections for 2015–2099 were downscaled, bias-corrected to the 1979– 2014 climate observation data (Abatzoglou 2013), and disaggregated to a 3-h timescale. Downscaling and disaggregation details are provided in Buotte et al. (2019b).

The number of years with low annual allocation to stem growth and/or annual net primary productivity of 0 were used to determine forest vulnerability to drought stress (Buotte et al. 2019b). For each decade, we defined low vulnerability in grid cells with 0 yr of NPP = 0 and low allocation to growth, medium vulnerability in grid cells with 1 yr with NPP = 0 and/or 1-3 yr with low allocation to growth, and high vulnerability in grid cells with more than 1 yr with NPP = 0 and/or more than 3 yr with no allocation to growth (Buotte et al. 2019b). Grid cells were ranked with low, medium, or high vulnerability for both IPSL CM5A-MR and MIROC5 forced simulations. For every grid cell, we calculated vulnerability to fire based on the increase in simulated area burned in the future compared with the past, weighted by the simulated area burned in the past (Buotte et al. 2019b). Final drought and fire vulnerability rankings included uncertainty due to climate projections by incorporating the drought and fire vulnerability ranking from simulations using each of the two climate projections, such that (1) uncertain, one GCM simulation ranked as low and one simulation ranked as high; (2) low, both GCMs low; (3) med-low, one low and one medium; (4) medium, both GCMs medium; (5) med-high, one medium and one high; (6) high, both GCMs high.

Further details on vulnerability calculation and assessment relative to observed mortality are provided in Buotte et al. (2019b).

We determined potential carbon sequestration (Keith et al. 2009a) by running CLM with no prescribed harvest beyond 2014 and summing net ecosystem productivity (NEP) from 2020 to 2099, thereby allowing forest type, soil properties, climate, and CO<sub>2</sub> concentrations to determine productivity. We pooled cumulative NEP across all grid cells and defined three categories of potential carbon sequestration based on the highest onethird (>1.12  $\times$  10<sup>5</sup> g/m<sup>2</sup>), middle one-third, and lowest one- third ( $<3.27 \times 10^4$  g C/m<sup>2</sup>) of the distribution. We then ranked forested areas to identify low, medium, and high carbon preservation priority based on the spatial coincidence of low future vulnerability to drought and fire and potential carbon sequestration (Appendix S1: Fig. S2). Forests with low vulnerability to future drought and fire and the highest potential carbon sequestration were ranked as high priority for preservation as carbon preserves; low vulnerability and medium carbon sequestration potential were ranked as medium priority; all other combinations were ranked as low priority. Hereafter we refer to forest priority for preservation as carbon preserves as "carbon priority."

### Tree mortality from bark beetles

Tree mortality from bark beetle attack is an important disturbance in western U.S. forests, but not currently incorporated into CLM. We therefore addressed the potential for future beetle mortality by assessing recent historical beetle mortality (Berner et al. 2017b) and existing future projections of climate suitability for beetle outbreaks (Bentz et al. 2010, Buotte et al. 2017) across our three forest carbon priority rankings.

## Above- and belowground carbon stocks

We assessed observation-based estimates of carbon stocks (i.e., not our simulated carbon stocks) across forests in each carbon priority ranking. We used the Regridded Harmonized World Soil Database V1.2 (Weider et al. 2014) for belowground carbon stocks, and a gridded data set of aboveground carbon stocks based on field measurements and remote sensing (Wilson et al. 2013).

## Species richness and critical habitat

We examined several aspects of biodiversity across forests with low, medium, and high carbon preservation priority. We acquired published tree species richness maps for the United States (Jenkins et al. 2015), species habitat maps for terrestrial vertebrates (amphibians, reptiles, birds, and mammals) from the U.S. Geological Survey Gap Analysis Program (USGS National Gap Analysis Program 2018), and species habitat maps identifying critical habitat by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2018). Each map was resampled to the  $4 \times 4$  km CLM grid. We computed terrestrial vertebrate species richness by taxa and across taxa for each grid cell. We also identified whether a terrestrial vertebrate species was listed as threatened or endangered (T&E) by the U.S. Fish and Wildlife Service and then reassessed species richness for this subset of species. Last, we summarized these aspects of species richness and critical habitat by forest carbon priority rank.

## RESULTS

# High-priority forest distribution and contribution to emissions mitigation

The high-carbon-priority forests are primarily along the Pacific coast and the Cascade Mountains, with scattered occurrences in the northern Rocky Mountains of Idaho and Montana (Fig. 1). Forests with medium carbon priority are more widely scattered throughout the western United States (Fig. 1).

High-carbon-priority forests cover  $132,016 \text{ km}^2$  or 10.3% of the forested domain and have the potential to sequester 4,815-5,450 Tg CO<sub>2</sub> equivalent (Tg CO<sub>2</sub> e; 1,312-1,485 Tg C) in aboveground carbon between 2020 and 2099 (Fig. 1, Table 1, Appendix S1: Table S1). Medium-carbon-priority forests cover 9.5% of the forested domain and could sequester 1,842-2,136 Tg CO<sub>2</sub> e (502–582 Tg C). Low-carbon-priority forests cover 80.2% of the forested domain and could sequester 12,789-16,533

Tg  $CO_2$  e (3,485–4,505 Tg C) by 2099. However, because the low-carbon-priority forests have higher future vulnerability, their carbon sequestration potential is less certain.

# Co-benefits of preserving high-carbon-priority forests

The forests we identified with the greatest potential to sequester carbon during this century provide multiple ecological co-benefits. Recent tree mortality from bark beetle attack was the lowest in these high-carbon-priority forests (Appendix S1: Fig. S3). These forests have the highest average present-day soil carbon stocks (14%) higher than medium and 65% higher than low carbon priority) and aboveground carbon stocks (41% higher than medium and 248% higher than low carbon priority; Fig. 2), and also currently support the highest tree species richness (Fig. 3). Furthermore, high-carbon-priority forests contain the highest proportional area of terrestrial vertebrate habitat for species listed as threatened or endangered by the U.S. Fish and Wildlife Service (Fig. 4), as well as the highest proportion of habitat designated as critical for threatened or endangered species survival (Fig. 4). There is less distinction in terrestrial vertebrate species richness by carbon priority rank, though high-carbon-priority forests tend to have higher amphibian and lower reptilian richness than forests with medium or low carbon priority ranks (Appendix S1: Fig. S4). It is important to highlight that the spatial

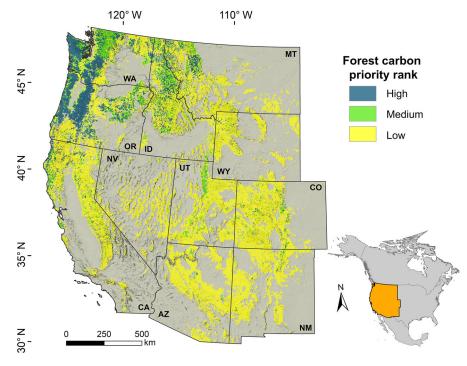


FIG. 1. Forested land in the western conterminous United States classified into priority for preservation to mitigate climate change based on the spatial co-occurrence of low vulnerability to drought and fire and low, medium, and high potential carbon sequestration. WA, Washington; ID, Idaho; MT, Montana; OR, Oregon; CA, California; NV, Nevada; UT, Utah; CO, Colorado; AZ, Arizona; NM, New Mexico.

Priority ranking	Area (km <sup>2</sup> )	Forested domain (%)	Carbon sequestration potential during 2020–2099 (Tg CO <sub>2</sub> e)†	Carbon sequestration potential during 2020–2099 (Tg C/km <sup>2</sup> )
High	132,016	10.3	4,815–5,450 (1,312–1,485 Tg C)	0.036–0.041
Medium	120,800	9.5	1,842–2,136 (502–582 Tg C)	0.015-0.018
Low	1,023,872	80.2	12,789–16,533 (3,485–4,505 Tg C)	0.012-0.016

TABLE 1. Area, percentage of forested domain, and carbon sequestration potential during 2020–2099 (calculated as the sum of annual net ecosystem production, with business-as-usual harvest amounts) in each priority category.

† Tg CO<sub>2</sub> equivalent. Values in parentheses are Tg CO<sub>2</sub>.

distribution of species richness (Appendix S1: Fig. S5) indicates some areas of exceptionally high species richness (e.g., the Klamath region in southern Oregon and northern California) have a low carbon priority ranking due to medium to high future vulnerability, particularly to fire, or low forest productivity. Summaries of species richness and habitat area by state are provided in Appendix S1: Figs. S6 and S7.

## DISCUSSION

Hotter and drier conditions are expected to increase future tree mortality from drought (Allen et al. 2010, McDowell et al. 2016) and fire (Spracklen et al. 2009, Pechony and Shindell 2010) in parts of the western United States, thus preserving forests with the lowest vulnerability to future disturbance is one intuitive component of a land preservation strategy. Forest preservation offers a cost-effective strategy to avoid and mitigate CO<sub>2</sub> emissions by increasing the magnitude of the terrestrial carbon sink in trees and soil, preserve biodiversity, and sustain additional ecosystem services (Griscom et al. 2017). We show considerable potential for forests in the western United States to sequester additional carbon over the coming century and demonstrate that protecting high-carbon-priority areas could help preserve components of biodiversity. However, we also find high biodiversity in some areas with low future carbon sequestration potential due to slow growth or high vulnerability to fire. We therefore suggest that developing area-based retention targets (Maron et al. 2018) for both carbon and biodiversity metrics, along with the consideration of land ownership (Krankina et al. 2014), would allow the development of a portfolio of preserves to meet these criteria.

Preserving high-carbon-priority forests avoids future CO<sub>2</sub> emissions from harvesting and mitigates existing emissions through carbon sequestration. Regional fossil fuel emissions averaged ~260 Tg C/yr from 2003 to 2012 according to the U.S. Energy Information Administration (2015). Preserving the high-carbon-priority forests in the western United States would account for approximately 6 yr of regional fossil fuel emissions, or 18-20% of the global mitigation potential of natural forest management solutions Griscom et al. (2017) identified for the combination of temperate and boreal forests by 2099. This would increase to almost 8 yr of regional emissions, or 27-32% of temperate and boreal forest mitigation potential, if preservation was expanded to include medium-carbon-priority forests. Carbon dioxide emissions from soils in degraded forests account for roughly 11% of global net emissions (Houghton and Nassikas 2017). As the high-carbon-priority forests have the highest soil carbon, preserving these forests avoids

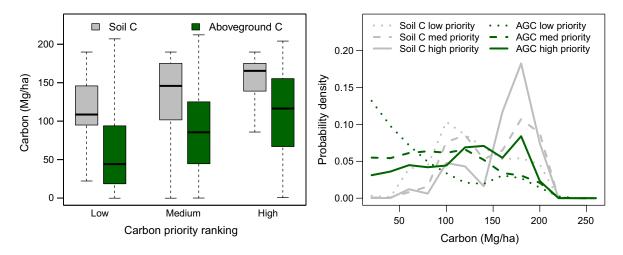


FIG. 2. Conterminous western U.S. forests ranked with the highest priority for preservation for carbon sequestration also have the highest current soil and aboveground carbon stocks. Carbon stocks from gridded measurements interpolated from observations (see *Materials and Methods*). Box plot components are mid line, median; box edges, first and third quartiles; and whiskers, max and min.

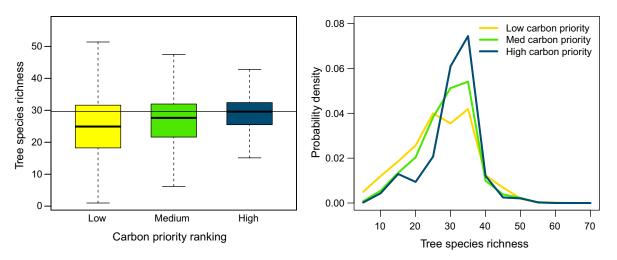


FIG. 3. Conterminous western U.S. forests ranked with the highest priority for preservation for carbon sequestration also have the highest present-day tree species richness (BioDiversityMapping.org richness data).

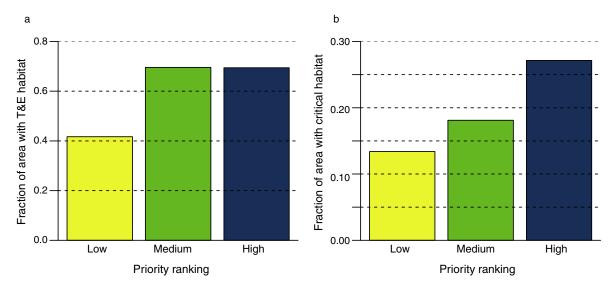


FIG. 4. Fraction of forest in each carbon priority ranking with (a) habitat of all threatened and endangered (T&E) species designated as critical for that species survival and (b) habitat of terrestrial vertebrate species listed as threatened or endangered by the U.S. Fish and Wildlife Service.

additional CO<sub>2</sub> emissions from the soil as surface litter and root material decay after harvest.

We found that high-carbon-priority forests in the western United States exhibit features of older, intact forests with high structural diversity (Keith et al. 2009b, Krankina et al. 2014), including carbon density and tree species richness. Forest resilience and adaptive capacity increase with increasing plant species richness (Morin et al. 2018, Watson et al. 2018), suggesting that preserving the high-carbon-priority forests would provide an added buffer against potential ecosystem transformation to future climate change.

Intact forests are particularly important for watershed protection by regulating soil permeability, overland flow, and erosion (DellaSala et al. 2011, Creed et al. 2016, Moomaw et al. 2019). Across the United States, National Forests are the largest source of drinking water (Furniss et al. 2010). In the Pacific Northwest, conversion of old-growth forests to plantations reduced summer stream flow by an average of 50% (Perry and Jones 2017). Preserving intact forests would provide the greatest benefit to watershed protection and clean water supply (DellaSala et al. 2011). Unfortunately, the area of forest interior (defined as forest area per land area) is declining faster than the total area of forest in the United States (Riitters and Wickham 2012). Remaining primary and intact forests need to be identified and incorporated in land management policies.

Recent studies have found positive relationships between carbon density and biodiversity across multiple biomes (Brandt et al. 2014, Lecina-Diaz et al. 2018), but also weak relationships at the stand scale (Sabatini et al. 2019). We show that preserving forests in the western United States with high productivity and low vulnerability to future fire and drought can aid in the maintenance of vertebrate biodiversity, as these forests contain the highest proportion of critical habitat for threatened and endangered species. Because extinction rates are expected to increase with projected climate change (Segan et al. 2016), preserving critical habitat is an important consideration for maintaining biodiversity. Our analysis also shows that benefits to biodiversity depend in part on the biodiversity metric. For example, we found amphibian richness was the highest in forests we identified with high carbon priority, likely because these forests occur most often in the moist maritime climate suitable to amphibians. On the other hand, these wet, high-carbon-priority forests tend to have lower reptile diversity than low-carbon-priority forests, such as those in the Southwest where reptile diversity was highest. We show that spatial overlap in measures of biodiversity and potential carbon sequestration occurs such that land management policies can optimize both priorities. However, we also demonstrate that areas of high biodiversity are found in medium to low-carbon-priority forests. Therefore, sound land preservation strategies need to include multiple priority metrics (Brandt et al. 2014).

Indeed, preservation of carbon-dense primary (Mackey et al. 2015) and intact forests (Watson et al. 2018) is a critical but insufficient criterion for maintaining biodiversity. Secondary forests can support high biodiversity (Donato et al. 2009, Gilroy et al. 2014), as well as different species assemblages compared with primary forests (Ferreira et al. 2018). There are regions identified as globally significant centers of biodiversity (Olson et al. 2012; e.g., the Klamath-Siskiyou region in southwest Oregon) that we identified with medium to high future vulnerability due to fire. Therefore, when protecting biodiversity is a high conservation priority, disturbance-prone forests will need to be included in areabased targets (Maron et al. 2018). Regional assessments (Dass et al. 2018) that simulate vegetation transformation on multi-decadal timescales are needed to elucidate the effect of future disturbance regimes on plant community composition in order to assess potential future biodiversity and determine preservation priority rankings of disturbance-prone forests.

Because secondary forests also arise from a legacy of human intervention, conservation of managed landscapes will be an important component of policies to maintain biodiversity and enhance climate mitigation (Kremen and Merenlender 2018). Regional analyses have shown that lengthening harvest cycles can substantially improve carbon sequestration (Law et al. 2018) and biodiversity (Gilroy et al. 2014) and therefore provide pathways for additional climate mitigation (Griscom et al. 2017). Historical stand structure analysis indicates young trees may have played an important role in buffering against particular types of disturbance (Baker and Williams 2015). However, because young trees can be more vulnerable to drought stress than mature trees (Irvine et al. 2002), assessments of future climate vulnerability of young forests will be a critical factor when evaluating harvest strategies (Nolan et al. 2018b). Regional dynamic vegetation simulations with explicit treatment of forest regeneration are necessary to assess the effects of land management scenarios and develop strategies for managed lands.

Assessing the potential for future forest carbon sequestration has inherent uncertainties concerning realized future climate, forest growth, and sources of forest mortality. We address uncertainties in future climate by using two climate scenarios that span a wide range of variability in temperature and precipitation (Buotte et al. 2019b), though we acknowledge that future climate remains uncertain due to the trajectory of carbon emissions, climate sensitivity to these emissions, and climate feedbacks (Collins et al. 2014, Schuur et al. 2015). Furthermore, simulated forest growth depends on how the model was parameterized (White et al. 2000). Here, we used parameterizations developed specifically for forest types in the western United States (Hudiburg et al. 2013, Law et al. 2018, Buotte et al. 2019b), which improved model agreement with historical observations as compared with more general forest type parameterizations (Buotte et al. 2019b). In response to increasing CO<sub>2</sub> concentration, trees may increase their water use efficiency (Keenan et al. 2013, Schimel et al. 2015), however, this response may depend on nutrient availability (Oren et al. 2001, Norby et al. 2010). The CLM incorporates nitrogen limitation (Oleson et al. 2013), which allows the CLM to accurately simulate recent changes in NPP observed under increasing CO<sub>2</sub> concentrations (Smith et al. 2016).

Mountain pine beetles (Dendroctonus ponderosae) were responsible for the majority of tree mortality from beetles in the recent past (Meddens et al. 2012). Previous analysis (Buotte et al. 2019b) indicates our drought metric identifies forests vulnerable to beetle attack due to the presence of drought-stressed trees (Boone et al. 2011), increasing our confidence in our vulnerability metric's ability to capture this important disturbance agent. Importantly, future projections of beetle population dynamics (Bentz et al. 2010) do not indicate increasing beetle populations in areas we define with high carbon priority. Climate suitability for tree mortality from mountain pine beetles is projected to increase in some high-elevation whitebark pine forests (Buotte et al. 2017), which we ranked with low carbon priority due to lower carbon sequestration potential, or medium to high vulnerability to future drought or fire. Predictive models of beetle population dynamics for multiple beetle species, that include host tree status when appropriate, would increase our ability to incorporate specific spatial representation of future forest vulnerability to beetle attack. We simulated future fire, but the model does not capture the potential for anomalous mega-fires.

Therefore, our estimates of future carbon sequestration potential in the absence of large-scale mortality events are likely to be robust.

Preservation of high carbon density Pacific Northwest forests that are also economically valuable for timber production will have costs and benefits to consider, including socioenvironmental benefits, the feasibility of preservation, and opportunity costs harvest. There is tremendous potential for proforestation, growing existing forests intact to their ecological potential, which is an effective, immediate, and low-cost approach to removing carbon dioxide from the atmosphere (Moomaw et al. 2019). Proforestation serves the greatest public good by maximizing co-benefits such as biological carbon sequestration and unparalleled ecosystem services including biodiversity enhancement, water and air quality, flood and erosion control, and low impact recreation. The development of governance programs to promote forest preservation will be critical. Our study is a first step at identifying areas with the highest potential for natural co-benefits and proforestation.

## CONCLUSIONS

If we are to avert our current trajectory toward massive global change, we need to make land stewardship a higher societal priority (Chan et al. 2016). Preserving temperate forests in the western United States that have medium to high potential carbon sequestration and low future climate vulnerability could account for approximately 8 yr of regional fossil fuel emissions, or 27-32% of the global mitigation potential previously identified for temperate and boreal forests, while also promoting ecosystem resilience and the maintenance of biodiversity. Biodiversity metrics also need to be included when selecting preserves to ensure species-rich habitats that result from frequent disturbance regimes are not overlooked. The future impacts of climate change, and related pressures as human population exponentially expands, make it essential to evaluate conservation and management options on multi-decadal timescales, with the shared goals of mitigating committed CO<sub>2</sub> emissions, reducing future emissions, and preserving plant and animal diversity to limit ecosystem transformation and permanent losses of species.

## ACKNOWLEDGMENTS

This research was supported by the Agriculture and Food Research Initiative of the U.S. Department of Agriculture National Institute of Food and Agriculture (Grants 2013-67003-20652, 2014-67003-22065, and 2014-35100-22066) for our North American Carbon Program studies, "Carbon cycle dynamics within Oregon's urban-suburban-forested-agricultural landscapes" and "Forest die-off, climate change, and human intervention in western North America," (and the U.S. Department of Energy (Grant DE-SC0012194). High-performance computing resources to run CLM on Cheyenne (https://doi.org/10.5065/d6rx99hx) were provided by NCAR's Computational and Information Systems Laboratory, sponsored by the National Science Foundation.

#### LITERATURE CITED

- Abatzoglou, J. T. 2013. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology 33:121–131.
- Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest/woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences USA 95:14839–14842.
- Allen, C. D., et al. 2010. A global overview of drought and heatinduced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.
- Baker, W. L., and M. A. Williams. 2015. Bet-hedging dry-forest resilience to climate-change threats in the western USA based on historical forest structure. Frontiers in Ecology and Evolution 2:1–7.
- Barnosky, A. D., et al. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602–613.
- Berner, L. T., and B. E. Law. 2016. Plant traits, productivity, biomass and soil properties from forest sites in the Pacific Northwest, 1999-2014. Nature Scientific Data 3:1–14.
- Berner, L. T., B. E. Law, and T. W. Hudiburg. 2017a. Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. Biogeosciences 14:365–378.
- Berner, L. T., B. E. Law, A. J. H. Meddens, and J. A. Hicke. 2017b. Tree mortality from fires, bark beetles, and timber harvest during a hot and dry decade in the western United States (2003-2012). Environmental Research Letters 12:065005.
- Boone, C. K., B. H. Aukema, J. Bohlmann, A. L. Carroll, and K. F. Raffa. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Canadian Journal of Forest Research 41:1174–1188.
- Brandt, P., D. J. Abson, D. A. DellaSala, R. Feller, and H. von Wehrden. 2014. Multifunctionality and biodiversity: ecosystem services in temperate rainforests of the Pacific Northwest, USA. Biological Conservation 169:362–371.
- Bright, R. M., E. Davin, T. O'Halloran, J. Pongratz, K. G. Zhao, and A. Cescatti. 2017. Local temperature response to land cover and management change driven by non-radiative processes. Nature Climate Change 7:296.
- Buotte, P. C., J. A. Hicke, H. K. Preisler, J. T. Abatzoglou, K. F. Raffa, and J. A. Logan. 2017. Recent and future climate suitability for whitebark pine mortality from mountain pine beetles varies across the western US. Forest Ecology and Management 399:132–142.
- Buotte, P. C., S. Levis, and B. E. Law. 2019a. NACP: forest carbon stocks, fluxes and productivity estimates, western USA, 1979-2099. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ornldaac/1662
- Buotte, P. C., S. Levis, B. E. Law, T. W. Hudiburg, D. E. Rupp, and J. J. Kent. 2019b. Near-future forest vulnerability to drought and fire varies across the western United States. Global Change Biology 25:290–303.
- Cameron, D. R., D. C. Marvin, J. M. Remucal, and M. C. Passero. 2017. Ecosystem management and land conservation can substantially contribute to California's climate mitigation goals. Proceedings of the National Academy of Sciences USA 114:12833–12838.
- Canadell, J. G., and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science 320:1456–1457.

- Canadell, J. G., C. Le Quere, M. R. Raupach, C. B. Field, E. T. Buitenhuis, P. Ciais, T. J. Conway, N. P. Gillett, R. A. Houghton, and G. Marland. 2007. Contributions to accelerating atmospheric CO2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences USA 104:18866–18870.
- Chan, K. M. A., et al. 2016. Why protect nature? Rethinking values and the environment. Proceedings of the National Academy of Sciences USA 113:1462–1465.
- Collins, M., et al. 2014. Long-term climate change: projections, commitments and irreversibility. Pages 1029–1136 in T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Climate change 2013: the physical science basis. IPCC, Cambridge, UK, New York, New York, USA.
- Creed, I. F., M. Weber, F. Accatino, and D. P. Kreutzweiser. 2016. Managing forests for water in the Anthropocene—the best kept secret services of forest ecosystems. Forests 7:60.
- Dass, P., B. Z. Houlton, Y. P. Wang, and D. Warlind. 2018. Grasslands may be more reliable carbon sinks than forests in California. Environmental Research Letters 13:074027.
- Davis, M., S. Faurby, and J.-C. Svenning. 2018. Mammal diversity will take millions of years to recover from the current biodiversity crisis. Proceedings of the National Academy of Sciences USA 115:11262–11267.
- DellaSala, D. A., J. R. Karr, and D. M. Olson. 2011. Roadless areas and clean water. Journal of Soil and Water Conservation 66:78A–84A.
- Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology 97:142–154.
- Eldenshenk, J., B. Schwind, K. Brewer, Z. Zhu, B. Quayle, and S. Howard. 2007. A project for monitoring trends in burn severity. Fire Ecology Special Issue 3:3–21.
- Ferreira, J., et al. 2018. Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nature. Climate Change 8:744.
- Furniss, M. J., et al. 2010. Water, climate change, and forests: watershed stewardship for a changing climate. PNW\_GTR\_812. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Gilroy, J. J., P. Woodcock, F. A. Edwards, C. Wheeler, B. L. G. Baptiste, C. A. M. Uribe, T. Haugaasen, and D. P. Edwards. 2014. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. Nature Climate Change 4:503–507.
- Griscom, B. W., et al. 2017. Natural climate solutions. Proceedings of the National Academy of Sciences USA 114:11645– 11650.
- Houghton, R. A., and A. A. Nassikas. 2017. Global and regional fluxes of carbon from land use and land cover change 1850-2015. Global Biogeochemical Cycles 31:456–472.
- Hudiburg, T., B. Law, D. P. Turner, J. Campbell, D. C. Donato, and M. Duane. 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecological Applications 19:163–180.
- Hudiburg, T. W., B. E. Law, C. Wirth, and S. Luyssaert. 2011. Regional carbon dioxide implications of forest bioenergy production. Nature Climate Change 1:419–423.
- Hudiburg, T. W., B. E. Law, and P. E. Thornton. 2013. Evaluation and improvement of the Community Land Model (CLM4) in Oregon forests. Biogeosciences 10:453–470.
- Hurrell, J. W., et al. 2013. The Community Earth System Model A Framework for Collaborative Research. Bulletin of the American Meteorological Society 94:1339–1360.

- IPCC. 2018. Summary for policymakers. in V. Masson-Delmotte, P. Zhai, H.-O. P-rtner, D. Roberts, J. Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. PÕan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield, editors. Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above preindustrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. World Meteorological Organization, Geneva, Switzerland, 32 pp.
- Irvine, J., B. E. Law, P. M. Anthoni, and F. C. Meinzer. 2002. Water limitations to carbon exchange in old-growth and young ponderosa pine stands. Tree Physiology 22:189–196.
- Jenkins, C. N., K. S. Van Houtan, S. L. Pimm, and J. O. Sexton. 2015. US protected lands mismatch biodiversity priorities. Proceedings of the National Academy of Sciences USA 112:5081–5086.
- Keenan, T. F., D. Y. Hollinger, G. Bohrer, D. Dragoni, J. W. Munger, H. P. Schmid, and A. D. Richardson. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499:324.
- Keith, H., R. Leuning, K. L. Jacobsen, H. A. Cleugh, E. van Gorsel, R. J. Raison, B. E. Medlyn, A. Winters, and C. Keitel. 2009a. Multiple measurements constrain estimates of net carbon exchange by a Eucalyptus forest. Agricultural and Forest Meteorology 149:535–558.
- Keith, H., B. G. Mackey, and D. B. Lindenmayer. 2009b. Reevaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proceedings of the National Academy of Sciences USA 106:11635–11640.
- Krankina, O. N., D. A. DellaSala, J. Leonard, and M. Yatskov. 2014. High-biomass forests of the Pacific Northwest: who manages them and how much is protected? Environmental Management 54:112–121.
- Kremen, C., and A. M. Merenlender. 2018. Landscapes that work for biodiversity and people. Science 362:eaau6020.
- Law, B. E., T. W. Hudiburg, L. T. Berner, J. Kent, P. C. Buotte, and M. E. Harmon. 2018. Land use strategies to mitigate climate change in carbon dense temperate forests. Proceedings of the National Academy of Sciences USA 115:3663–3668.
- Le Quere, C., et al. 2018. Global carbon budget 2018. Earth System Science Data 10:2141–2194.
- Lecina-Diaz, J., A. Alvarez, A. Regos, P. Drapeau, A. Paquette, C. Messier, and J. Retana. 2018. The positive carbon stocksbiodiversity relationship in forests: co-occurrence and drivers across five subclimates. Ecological Applications 28:1481– 1493.
- Mackey, B., et al. 2015. Policy Options for the World's Primary Forests in Multilateral Environmental Agreements. Conservation Letters 8:139–147.
- Maron, M., J. S. Simmonds, and J. E. M. Watson. 2018. Bold nature retention targets are essential for the global environment agenda. Nature Ecology & Evolution 2:1194–1195.
- McDowell, N. G., et al. 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. Nature Climate Change 6:295–300.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, D.C., USA.
- Meddens, A. J. H., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecological Applications 22:1876–1891.

- Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.
- Mitchell, T. D., and P. D. Jones. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. International Journal of Climatology 25:693–712.
- Moomaw, W. R., S. Masino, and E. K. Falson. 2019. Intact forests in the United States: proforestation mitigates climate change and serves the greatest good. Frontiers in Forests and Global Change 2:1–10.
- Morin, X., L. Fahse, H. Jactel, M. Scherer-Lorenzen, R. Garcia-Valdes, and H. Bugmann. 2018. Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. Scientific Reports 8: 1–12.
- Nolan, C., et al. 2018*a*. Past and future global transformation of terrestrial ecosystems under climate change. Science 361:920–923.
- Nolan, R. H., D. M. Drew, A. P. O'Grady, E. A. Pinkard, K. Paul, S. H. Roxburgh, P. J. Mitchell, J. Bruce, M. Battaglia, and D. Ramp. 2018b. Safeguarding reforestation efforts against changes in climate and disturbance regimes. Forest Ecology and Management 424:458–467.
- Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. McMurtrie. 2010. CO2 enhancement of forest productivity constrained by limited nitrogen availability. Proceedings of the National Academy of Sciences USA 107:19368–19373.
- Oleson, K. W., et al. 2013. Technical description of version 4.5 of the Community Land Model (CLM). National Center for Atmospheric Research, Boulder, Colorado, USA.
- Olson, D., D. A. DellaSala, R. F. Noss, J. R. Strittholt, J. Kass, M. E. Koopman, and T. F. Allnutt. 2012. Climate change refugia for biodiversity in the Klamath-Siskiyou Ecoregion. Natural Areas Journal 32:65–74.
- Oren, R., et al. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. Nature 411:469–472.
- Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8:715–732.
- Pearson, R. G., S. J. Phillips, M. M. Loranty, P. S. A. Beck, T. Damoulas, S. J. Knight, and S. J. Goetz. 2013. Shifts in Arctic vegetation and associated feedbacks under climate change. Nature Climate Change 3:673–677.
- Pechony, O., and D. T. Shindell. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. Proceedings of the National Academy of Sciences USA 107:19167–19170.
- Perry, T. D., and J. A. Jones. 2017. Summer streamflow deficits from regenerating Douglas-fir forest in the Pacific Northwest, USA. Ecohydrology 10:e1790.
- Peters, G. P., R. M. Andrew, T. Boden, J. G. Canadell, P. Ciais, C. Le Quere, G. Marland, M. R. Raupach, and C. Wilson. 2013. COMMENTARY: the challenge to keep global warming below 2 degrees C. Nature Climate Change 3:4–6.
- Rehfeldt, G. E., N. L. Crookston, M. V. Warwell, and J. S. Evans. 2006. Empirical analyses of plant-climate relationships for the western United States. International Journal of Plant Sciences 167:1123–1150.
- Resplandy, L., R. F. Keeling, Y. Eddebbar, M. K. Brooks, R. Wang, L. Bopp, M. C. Long, J. P. Dunne, W. Koeve, and A. Oschlies. 2018. Quantification of ocean heat uptake from changes in atmospheric O2 and CO2 composition. Nature 563:105–108.

- Riitters, K. H., and J. D. Wickham. 2012. Decline of forest interior conditions in the conterminous United States. Scientific Reports 2:1–4.
- Rogelj, J., M. den Elzen, N. Hohne, T. Fransen, H. Fekete, H. Winkler, R. S. Chaeffer, F. Ha, K. Riahi, and M. Meinshausen. 2016. Paris Agreement climate proposals need a boost to keep warming well below 2 degrees C. Nature 534:631–639.
- Sabatini, F. M., et al. 2019. Trade-offs between carbon stocks and biodiversity in European temperate forests. Global Change Biology 25:536–548.
- Schimel, D., B. B. Stephens, and J. B. Fisher. 2015. Effect of increasing CO2 on the terrestrial carbon cycle. Proceedings of the National Academy of Sciences USA 112:436–441.
- Schuur, E. A. G., et al. 2015. Climate change and the permafrost carbon feedback. Nature 520:171–179.
- Segan, D. B., K. A. Murray, and J. E. M. Watson. 2016. A global assessment of current and future biodiversity vulnerability to habitat loss-climate change interactions. Global Ecology and Conservation 5:12–21.
- Settele, J., R. Scholes, R. Betts, S. E. Bunn, P. Leadley, D. Nepstad, J. T. Overpeck, and M. A. Taboada. 2014. Terrestrial and inland water systems. Pages 271–359 *in* C. B. Field, et al., editors. Climate change 2014: impacts, adaptation, and vulnerability. Part a: global and sectoral aspects. Contribution of working group ii to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK.
- Smith, W. K., S. C. Reed, C. C. Cleveland, A. P. Ballantyne, W. R. L. Anderegg, W. R. Wieder, Y. Y. Liu, and S. W. Running. 2016. Large divergence of satellite and Earth system model estimates of global terrestrial CO2 fertilization. Nature Climate Change 6:306–310.
- Smith, P., J. Price, A. Molotoks, R. Warren, and Y. Malhi. 2018. Impacts on terrestrial biodiversity of moving from a 2 degrees C to a 1.5 degrees C target. Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences 376.
- Solomon, S., G. K. Plattner, R. Knutti, and P. Friedlingstein. 2009. Irreversible climate change due to carbon dioxide emissions. Proceedings of the National Academy of Sciences USA 106:1704–1709.
- Spracklen, D. V., L. J. Mickley, J. A. Logan, R. C. Hudman, R. Yevich, M. D. Flannigan, and A. L. Westerling. 2009. Impacts of climate change from 2000 to 2050 on wildfire activity and carbonaceous aerosol concentrations in the western United States. Journal of Geophysical Research: Atmospheres 114:1–17.
- Steffen, W., et al. 2018. Trajectories of the Earth System in the Anthropocene. Proceedings of the National Academy of Sciences USA 115:8252–8259.
- United Nations Framework Convention on Climate Change (UNFCC). 2015. The Paris Agreement. UNFCC, Paris, France.
- United Nations General Assembly. 2015. Transforming our world: the 2030 agenda for sustainable development. United Nations General Assembly, New York, New York, USA.
- U.S. Energy Information Administration. 2015. Energy-related carbon dioxide emissions at the state level, 2000–2013. U.S. Department of Energy, Washington, D.C., USA.
- U.S. Fish and Wildlife Service. 2018. U.S. FWS threatened & endangered species active critical habitat report. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- USGS National Gap Analysis Program. 2018. Gap analysis project species habitat maps CONUS. U.S. Geological Survey, Reston, Virginia, USA.
- Watson, J. E. M., et al. 2018. The exceptional value of intact forest ecosystems. Nature Ecology & Evolution 2:599–610.

- Weider, W. R., J. Boehnert, G. B. Bonan, and M. Langseth. 2014. Regridded harmonized world soil database. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: net primary production controls. Earth Interactions 4:1–85.
- Whittier, T. R., and A. N. Gray. 2016. Tree mortality based fire severity classification for forest inventories: a Pacific North-

west national forests example. Forest Ecology and Management 359:199-209.

- Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and disappearing climates by 2100 AD. Proceedings of the National Academy of Sciences USA 104:5738–5742.
- Wilson, B. T., C. W. Woodall, and D. M. Griffith. 2013. Imputing forest carbon stock estimates from inventory plots to a nationally continuous coverage. Carbon Balance and Management 8:15.

#### SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2039/full

# DATA AVAILABILITY

Simulated carbon fluxes are available from the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) at: https://doi.org/10.3334/ornldaac/1662