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

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|  | carbon sequestration potential but high biodiversity, underscoring the <br> need to consider multiple criteria when designing a land preservation <br> portfolio. Our work demonstrates how process models and ecological <br> criteria can be used to prioritize landscape preservation for mitigating <br> greenhouse gas emissions and preserving biodiversity in a rapidly <br> changing climate. |
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# Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States 

RH: Carbon sequestration and biodiversity

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#### 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. Highproductivity, low-vulnerability forests have the potential to sequester up to $5,450 \mathrm{TgCO}_{2}$ equivalent $(1,485 \mathrm{Tg} \mathrm{C})$ by 2099 , which is up to $20 \%$ of the global mitigation potential previously identified for all temperate and boreal forests, or up to $\sim 6$ years 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.


Keywords: carbon sequestration, biodiversity, process modeling, climate change, forest, mitigation, western US, Community Land Model (CLM)

## 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 degrees Celsius 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 two degrees Celsius (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 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. 2018a).

Along with emissions, multiple biogeophysical processes, including carbon uptake by the land and oceans and ocean heat exchange (Solomon et al. 2009), influence atmospheric $\mathrm{CO}_{2}$ (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 $\mathrm{CO}_{2}$ and chances of climate destabilization (Barnosky et al. 2012, Steffen et al. 2018). Land preservation and timber harvest management (natural climate 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 $2^{\circ} \mathrm{C}$ by 2039 (Griscom et al. 2017). Land management can also mitigate the negative effects that climate-induced ecosystem transformations have on biodiversity 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 $\mathrm{CO}_{2}$ 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 above ground 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 (Oleson et al. 2013) (CLM) to simulate the forest carbon cycle across the western US (Figure S1) at a $4 \times 4 \mathrm{~km}$ 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 (Figure 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 US (Buotte et al. 2019). In particular, these include specification of physiological parameters controlling photosynthesis for the dominant species in the major forest types (Figure S1) of the western US (Berner and Law 2016, Law et al. 2018, Buotte et al. 2019), enhanced drought sensitivity through species-specific stomatal response to soil moisture and leaf shedding during periods of drought stress (Buotte et al. 2019), and improved fire simulation by incorporating regional ignition probabilities and fuel load constraints (Buotte et al. 2019).

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 1901-1978 we forced CLM with CRUNCEP climate data (Mitchell and Jones 2005) statistically downscaled to $4 \times 4 \mathrm{~km}$ and bias corrected to our 1979-2014 climate data. Climate data from 1979-2014 were disaggregated from daily to 3-hourly intervals at $4 \times 4 \mathrm{~km}$ resolution (Abatzoglou 2013). Downscaling and disaggregation details are provided in Buotte et al.(2019). 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. 2019). 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 CA (Hudiburg et al. 2009, Hudiburg et al. 2011), 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. (2019), 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 US, simulated aboveground carbon was within one standard deviation of observation-based aboveground carbon (Obs. mean $=30.5 \mathrm{Mg} \mathrm{C} / \mathrm{ha}, \mathrm{SD}=39.7 \mathrm{Mg} \mathrm{C} / \mathrm{ha}, \mathrm{CLM}$ mean $=59.1 \mathrm{Mg}$ $\left.\mathrm{C} / \mathrm{ha}, \mathrm{SD}=45.5 \mathrm{Mg} \mathrm{C} / \mathrm{h}, \mathrm{R}^{2}=0.80\right)$. When grouped by forest type, simulated aboveground carbon was highly correlated with observations with a tendency towards higher simulated values
$\left(\mathrm{R}^{2}=0.84\right.$, mean bias error $\left.=4 \%\right)$. Over the forested domain, simulated area burned was highly correlated with observed area burned $\left(\mathrm{R}^{2}=0.75\right)$, 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. 2019). We selected IPSL-CM5AMR, which projects warm and dry future conditions, and MIROC5, which is close to the multimodel average for future temperature and precipitation across the western US (Buotte et al. 2019). Climate projections for 2015-2099 were downscaled, bias-corrected to the 1979-2014 climate observation data (Abatzoglou 2013), and disaggregated to 3-hourly timescale. Downscaling and disaggregation details are provided in Buotte et al. (2019).

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. 2019). For each decade, we defined low vulnerability in grid cells with 0 years of NPP $=0$ and low allocation to growth, medium vulnerability in grid cells with one year with NPP $=0$ and/or 1-3 years with low allocation to growth, and high vulnerability in grid cells with more than one year with NPP $=0$ and/or more than three years with no allocation to growth (Buotte et al. 2019). 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. 2019). 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. (2019).

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 20202099, thereby allowing forest type, soil properties, climate, and $\mathrm{CO}_{2}$ concentrations to determine productivity. We pooled cumulative NEP across all grid cells and defined three categories of potential carbon sequestration based on the highest third $\left(>1.12 \mathrm{e} 5 \mathrm{gCm}^{-2}\right)$, middle third, and lowest third $\left(<3.27 \mathrm{e} 4 \mathrm{gCm}^{-2}\right)$ 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 (Figure 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 US 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 below-ground 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 below-ground carbon stocks, and a gridded dataset of above-ground 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 US (Jenkins et al. 2015), species habitat maps for terrestrial vertebrates (amphibians, reptiles, birds, and mammals) from the US Geological Survey Gap Analysis Program(USGS National Gap Analysis Program 2018), and species habitat maps identifying critical habitat by the US Fish \& Wildlife Service (US Fish \& Wildlife Service 2018). Each map was resampled to the $4 \times 4 \mathrm{~km}$ 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 US Fish and Wildlife Service and then re-assessed species richness for this subset of species.

Lastly, 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 (Figure 1). Forests with medium carbon priority are more widely scattered throughout the western US (Figure 1).

High carbon priority forests cover $132,016 \mathrm{~km}^{2}$ or $10.3 \%$ of the forested domain and have the potential to sequester $4,815-5,450 \mathrm{TgCO}_{2} \mathrm{e}(1,312-1,485 \mathrm{TgC})$ in aboveground carbon between 2020-2099 (Figure 1, Table 1, Table S1). Medium carbon priority forests cover 9.5\% of the forested domain and could sequester 1,842-2,136 TgCO2e (502-582 TgC). Low carbon priority forests cover $80.2 \%$ of the forested domain and could sequester $12,789-16,533 \mathrm{TGCO}_{2} \mathrm{e}$ ( $3,485-4,505 \mathrm{TgC}$ ) 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 (Figure 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; Figure 2), and also currently support the highest tree species richness (Figure 3).

Furthermore, high carbon priority forests contain the highest proportional area of terrestrial vertebrate habitat for species listed as threatened or endangered by the US Fish \& Wildlife Service (Figure 4), as well as the highest proportion of habitat designated as critical for threatened or endangered species survival (Figure 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 (Figure S4). It is important to highlight that the spatial distribution of species richness (Figure 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 figures 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 US, 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 $\mathrm{CO}_{2}$ 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 US 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 $\mathrm{CO}_{2}$ emissions from harvesting and mitigates existing emissions through carbon sequestration. Regional fossil fuel emissions averaged $\sim 260 \mathrm{Tg}$ C / yr from 2003-2012 according to the US Energy Information Administration (2015). Preserving the high carbon priority forests in the western US would account for approximately six years 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 years 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 additional $\mathrm{CO}_{2}$ emissions from the soil as surface litter and root material decay after harvest.

We found that high carbon priority forests in the western US 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 US, 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 US (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 US 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 KlamathSiskiyou region in SW 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 area-based 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. 2019), 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 US (Hudiburg et al. 2013, Law et al. 2018, Buotte et al. 2019), which improved model agreement with historical observations as compared with more general forest type parameterizations (Buotte et al. 2019). In response to increasing CO 2 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 CO2 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. 2019) 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 towards massive global change, we need to make land stewardship a higher societal priority (Chan et al. 2016). Preserving temperate forests in the western US that have medium to high potential carbon sequestration and low future climate vulnerability could account for approximately eight years 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 $\mathrm{CO}_{2}$ emissions, reducing future emissions, and preserving plant and animal diversity to limit ecosystem transformation and permanent losses of species.

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## References

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 of the United States of America 95:14839-14842.
Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced 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.
Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, N. D. Martinez, A. Mooers, P. Roopnarine, G. Vermeij, J. W. Williams, R. Gillespie, J. Kitzes, C. Marshall, N. Matzke, D. P. Mindell, E. Revilla, and A. B. Smith. 2012. Approaching a state shift in Earth's biosphere. Nature 486:5258.

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.
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.
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 399:132142.

Buotte, P. C., S. Levis, B. E. Law, T. W. Hudiburg, D. E. Rupp, and J. J. Kent. 2019. 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 of the United States of America 114:12833-12838.

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 of the United States of America 104:18866-18870.
Canadell, J. G., and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science 320:1456-1457.
Chan, K. M. A., P. Balvanera, K. Benessaiah, M. Chapman, S. Diaz, E. Gomez-Baggethun, R. Gould, N. Hannahs, K. Jax, S. Klain, G. W. Luck, B. Martin-Lopez, B. Muraca, B. Norton, K. Ott, U. Pascual, T. Satterfield, M. Tadaki, J. Taggart, and N. Turner. 2016. Why protect nature? Rethinking values and the environment. Proceedings of the National Academy of Sciences of the United States of America 113:1462-1465.
Collins, M., R. Knutti, J. Arblaster, J.-L. Dufresne, T. Fichefet, P. Friedlingstein, X. Gao, W. J. Gutowski, Jr., T. Johns, G. Krinner, M. Shongwe, C. Tebaldi, A. J. Weaver, M. Wehner, M. R. Allen, T. Andrews, U. Beyerle, C. M. Bitz, S. Bony, B. B. B. Booth, H. E. Brooks, V. Brovkin, O. Browne, C. Brutel-Vuilmet, M. Cane, R. Chadwick, E. Cook, K. H. Cook, M. Eby, J. Fasullo, E. M. Fischer, C. E. Forest, P. Forster, P. Good, H. Goosse, J. M. Gregory, G. C. Hegerl, P. J. Hezel, K. I. Hodges, M. M. Holland, M. Huber, P. Huybrechts, M. Joshi, V. Kharin, Y. Kushnir, D. M. Lawrence, R. W. Lee, S. Liddicoat, C. Lucas, W. Lucht, J. Marotzke, F. Massonnet, H. D. Matthews, M. Meinshausen, C. Morice, A. Otto, C. M. Patricola, G. Philippon-Berthier, Prabhat, S. Rahmstorf, W. J. Riley, J. Rogelj, O. Saenko, R. Seager, J. Sedlacek, L. C. Shaffrey, D. Shindell, J. Sillmann, A. Slater, B. Stevens, P. A. Stott, R. Webb, G. Zappa, and K. Zickfeld. 2014. Long-term Climate Change: Projections, Commitments and Irreversibility. Climate Change 2013: the Physical Science Basis:1029-1136.
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.
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.
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 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.
Ferreira, J., G. D. Lennox, T. A. Gardner, J. R. Thomson, E. Berenguer, A. C. Lees, R. Mac Nally, L. Aragao, S. F. B. Ferraz, J. Louzada, N. G. Moura, V. H. F. Oliveira, R. Pardini, R. R. C. Solar, I. C. G. Vieira, and J. Barlow. 2018. Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nature Climate Change 8:744-+.
Furniss, M. J., B. P. Staab, S. Hazelhurst, F. Clifton, K. Roby, B. L. Ilhardt, E. B. Larry, A. H. Todd, L. M. Reid, S. J. Hines, K. A. Bennett, C. H. Luce, and P. J. Edwards. 2010. Water, climate change, and forests: watershed stewardship for a changing climate. PNW_GTR_812, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.

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., J. Adams, P. W. Ellis, R. A. Houghton, G. Lomax, D. A. Miteva, W. H. Schlesinger, D. Shoch, J. V. Siikamaki, P. Smith, P. Woodbury, C. Zganjar, A. Blackman, J. Campari, R. T. Conant, C. Delgado, P. Elias, T. Gopalakrishna, M. R. Hamsik, M. Herrero, J. Kiesecker, E. Landis, L. Laestadius, S. M. Leavitt, S. Minnemeyer, S. Polasky, P. Potapov, F. E. Putz, J. Sanderman, M. Silvius, E. Wollenberg, and J. Fargione. 2017. Natural climate solutions. Proceedings of the National Academy of Sciences of the United States of America 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, and P. E. Thornton. 2013. Evaluation and improvement of the Community Land Model (CLM4) in Oregon forests. Biogeosciences 10:453-470.
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.
Hurrell, J. W., M. M. Holland, P. R. Gent, S. Ghan, J. E. Kay, P. J. Kushner, J. F. Lamarque, W. G. Large, D. Lawrence, K. Lindsay, W. H. Lipscomb, M. C. Long, N. Mahowald, D. R. Marsh, R. B. Neale, P. Rasch, S. Vavrus, M. Vertenstein, D. Bader, W. D. Collins, J. J. Hack, J. Kiehl, and S. Marshall. 2013. The Community Earth System Model A Framework for Collaborative Research. Bulletin of the American Meteorological Society 94:13391360.

IPCC. 2018. Global warming of $1.5^{\circ}$ C. Incheon, Republic of Korea.
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 22:189196.

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 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. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proceedings of the National Academy of Sciences of the United States of America 106:1163511640.

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.
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. Proc. Natl Acad. Sci. USA 115:3663-3668.
Le Quere, C., R. M. Andrew, P. Friedlingstein, S. Sitch, J. Hauck, J. Pongratz, P. A. Pickers, J. I. Korsbakken, G. P. Peters, J. G. Canadell, A. Arneth, V. K. Arora, L. Barbero, A. Bastos, L. Bopp, F. Chevallier, L. P. Chini, P. Ciais, S. C. Doney, T. Gkritzalis, D. S. Goll, I. Harris, V. Haverd, F. M. Hoffman, M. Hoppema, R. A. Houghton, G. Hurtt, T. Ilyina, A. K. Jain, T. Johannessen, C. D. Jones, E. Kato, R. F. Keeling, K. K. Goldewijk, P. Landschuetzer, N. Lefevre, S. Lienert, Z. Liu, D. Lombardozzi, N. Metzl, D. R. Munro, J. E. M. S. Nabel, S.-i. Nakaoka, C. Neill, A. Olsen, T. Ono, P. Patra, A. Peregon, W. Peters, P. Peylin, B. Pfeil, D. Pierrot, B. Poulter, G. Rehder, L. Resplandy, E. Robertson, M. Rocher, C. Roedenbeck, U. Schuster, J. Schwinger, R. Seferian, I. Skjelvan, T. Steinhoff, A. Sutton, P. P. Tans, H. Tian, B. Tilbrook, F. N. Tubiello, I. T. van der Laan-Luijkx, G. R. van der Werf, N. Viovy, A. P. Walker, A. J. Wiltshire, R. Wright, S. Zaehle, and B. Zheng. 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 stocks-biodiversity relationship in forests: co-occurrence and drivers across five subclimates. Ecological Applications 28:1481-1493.
Mackey, B., D. A. DellaSala, C. Kormos, D. Lindenmayer, N. Kumpel, B. Zimmerman, S. Hugh, V. Young, S. Foley, K. Arsenis, and J. E. M. Watson. 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 2:11941195.

McDowell, N. G., A. P. Williams, C. Xu, W. T. Pockman, L. T. Dickman, S. Sevanto, R. Pangle, J. Limousin, J. Plaut, D. S. Mackay, J. Ogee, J. C. Domec, C. D. Allen, R. A. Fisher, X. Jiang, J. D. Muss, D. D. Breshears, S. A. Rauscher, and C. Koven. 2016. Multi-scale predictions of massive conifer mortality due to chronic temperature rise. Nature Climate Change 6:295-300.
MEA. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. Washington, D.C.
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.

Nolan, C., J. T. Overpeck, J. R. M. Allen, P. M. Anderson, J. L. Betancourt, H. A. Binney, S. Brewer, M. B. Bush, B. M. Chase, R. Cheddadi, M. Djamali, J. Dodson, M. E. Edwards, W. D. Gosling, S. Haberle, S. C. Hotchkiss, B. Huntley, S. J. Ivory, A. P. Kershaw, S.-H. Kim, C. Latorre, M. Leydet, A.-M. Lézine, K.-B. Liu, Y. Liu, A. V. Lozhkin, M. S. McGlone, R. A. Marchant, A. Momohara, P. I. Moreno, S. Müller, B. L. Otto-Bliesner, C. Shen, J. Stevenson, H. Takahara, P. E. Tarasov, J. Tipton, A. Vincens, C. Weng, Q. Xu, Z. Zheng, and S. T. Jackson. 2018a. 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 of the United States of America 107:19368-19373.
Oleson, K. W., D. M. Lawrence, G. B. Bonan, B. Drewniak, M. Huang, C. D. Koven, S. Levis, F. Li, W. J. Riley, Z. M. Subin, S. C. Swenson, P. E. Thornton, A. Bozbiyik, R. Fisher, E. Kluzek, J. F. Lamarque, L. R. Leung, W. Lipscomb, S. Muszala, D. M. Ricciuto, W. Sacks, J. Sun, J. Tang, and Z. Yang. 2013. Technical descriptioin of version 4.5 of the Community Land Model (CLM). National Center for Atmospheric Research, Boulder, CO.
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., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maier, K. V. R. Schafer, H. McCarthy, G. Hendrey, S. G. McNulty, and G. G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. Nature 411:469472.

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 of the United States of America 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.
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 02 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.
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., R. B. de Andrade, Y. Paillet, P. Odor, C. Bouget, T. Campagnaro, F. Gosselin, P. Janssen, W. Mattioli, J. Nascimbene, T. Sitzia, T. Kuemmerle, and S. Burrascano. 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 of the United States of America 112:436-441.
Schuur, E. A. G., A. D. McGuire, C. Schaedel, G. Grosse, J. W. Harden, D. J. Hayes, G. Hugelius, C. D. Koven, P. Kuhry, D. M. Lawrence, S. M. Natali, D. Olefeldt, V. E. Romanovsky, K. Schaefer, M. R. Turetsky, C. C. Treat, and J. E. Vonk. 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, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, and L. L. White, 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 of Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
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.

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.
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 of the United States of America 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.
Steffen, W., J. Rockstrom, K. Richardson, T. M. Lenton, C. Folke, D. Liverman, C. P. Summerhayes, A. D. Barnosky, S. E. Cornell, M. Crucifix, J. F. Donges, I. Fetzer, S. J. Lade, M. Scheffer, R. Winkelmann, and H. J. Schellnhuber. 2018. Trajectories of the Earth System in the Anthropocene. Proceedings of the National Academy of Sciences of the United States of America 115:8252-8259.

United Nations Framework Convention on Climate Change (UNFCC). 2015. The Paris Agreement. Paris.
United Nations General Assembly. 2015. Transforming Our World: the 2030 Agenda for Sustainable Development. New York.
US Energy Information Administration. 2015. Energy-related Carbon Dioxide Emissions at the State Level, 2000-2013. US Department of Energy, Washington, D.C.
US Fish \& Wildlife Service. 2018. U.S. FWS Threatened \& Endangered Species Active Critical Habitat Report.in U. F. W. Service, editor.
USGS National Gap Analysis Program. 2018. Gap Analysis Project Species Habitat Maps CONUS. U.S. Geological Survey.
Watson, J. E. M., T. Evans, O. Venter, B. Williams, A. Tulloch, C. Stewart, I. Thompson, J. C. Ray, K. Murray, A. Salazar, C. McAlpine, P. Potapov, J. Walston, J. G. Robinson, M. Painter, D. Wilkie, C. Filardi, W. F. Laurance, R. A. Houghton, S. Maxwell, H. Grantham, C. Samper, S. Wang, L. Laestadius, R. K. Runting, G. A. Silva-Chavez, J. Ervin, and D. Lindenmayer. 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 Northwest 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. Proc. Natl Acad. Sci. 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 8:1:15.

Table 1. Area, percent 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.

| Priority Ranking | Area <br> $\left(\mathrm{km}^{2}\right)$ | \% of <br> Forested <br> Domain | Carbon sequestration <br> potential during 2020- <br> 2099 in TgC and <br> $\left(\mathrm{TgCO}_{2} \mathrm{e}\right)$ | Carbon sequestration <br> potential during 2020- <br> 2099 in TgC/km |
| :--- | :---: | :---: | :---: | :---: |
| High | 132,016 | 10.3 | $4,815-5,450$ <br> $(1,312-1,485 \mathrm{TgC})$ | $0.036-0.041$ |
| Medium | 120,800 | 9.5 | $1,842-2,136$ <br> $(502-582 \mathrm{TgC})$ | $0.015-0.018$ |
| Low | $1,023,872$ | 80.2 | $12,789-16,533$ <br> $(3,485-4,505 \mathrm{TgC})$ | $0.012-0.016$ |

## Figure Legends

Figure 1. Forested land in the western conterminous US 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.

Figure 2. Conterminous western US 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 Methods).

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

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


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



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

## Ecological Applications

## Appendix S1

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

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Supplemental Information


Figure S1. Distribution of forest types simulated with the Community Land Model to determine forest vulnerability and carbon sequestration potential. Figure reprinted from Buotte et al. 2018.



Figure S2. Forested land in the western US classified by a) cumulative potential net ecosystem production during 2020-2099 and b) maximum vulnerability to drought or fire during 2020-2099.
(a)

(b)


Figure S3. (a) Percent of grid cells with bark beetle mortality during 1996-2012, with forest preservation priority determined from future vulnerability to drought and fire and potential carbon sequestration shown as colored points. Distinctions in point colors are most clearly visible when zoomed in. (b) Percent of each forest preservation priority class with beetle mortality during 19962012.


Figure S4. Species richness of all vertebrates and by taxa in left column and those species listed as threatened or endangered by the US Fish \& Wildlife Service in forests in the right column, in forests in each carbon priority ranking category.


Figure S5. Distribution of species richness across the western US by taxa. Data compiled from the National Gap Analysis program https://doi.org/10.5066/F7V122T2.


Figure S6. Mean species richness in each forest priority ranking by state. Species richness data from the National Gap Analysis Program. Sample size for calculating means is the number of grid cells in each priority ranking.


Figure S7. Area of habitat for species identified as Threatened or Endangered by the US Fish \& Wildlife Service, and area of habitat identified as critical for the recovery of species identified as Threatened or Endangered by the US Fish \& Wildlife Service in each forest priority ranking by state. Data shown in area (a,c) and percent of area (b.d).

Table S1. Area, percent of forested domain, and carbon sequestration potential during 2020-2099 in each carbon priority category (low, med, high) by state.

| State | Area (km ${ }^{2}$ ), \% of Forested Area (\%) Priority Ranking |  |  | Carbon sequestration potential during 2020-2099 (TgC) Priority Ranking |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Low | Med | High | Low | Medium | High |
| WA | $\begin{gathered} \hline 55,568 \\ (43.5) \\ \hline \end{gathered}$ | $\begin{gathered} 30,720 \\ (21.0) \\ \hline \end{gathered}$ | $\begin{aligned} & 41,552 \\ & (32.5) \\ & \hline \end{aligned}$ | $\begin{gathered} 326.1- \\ 371.1 \end{gathered}$ | $\begin{gathered} \hline 136.9- \\ 146.1 \\ \hline \end{gathered}$ | $\begin{gathered} 434.6- \\ 474.8 \end{gathered}$ |
| OR | $\begin{aligned} & 81,568 \\ & (51.3) \\ & \hline \end{aligned}$ | $\begin{gathered} 20,992 \\ (13.2) \\ \hline \end{gathered}$ | $\begin{gathered} 56,400 \\ (35.4) \\ \hline \end{gathered}$ | $\begin{gathered} 532.4- \\ 654.3 \\ \hline \end{gathered}$ | $\begin{aligned} & 87.6- \\ & 108.6 \end{aligned}$ | $\begin{gathered} \hline 562.7- \\ 676.2 \\ \hline \end{gathered}$ |
| CA | $\begin{gathered} 131,808 \\ (86.9) \\ \hline \end{gathered}$ | $\begin{gathered} 12,832 \\ (8.5) \\ \hline \end{gathered}$ | $\begin{aligned} & 7,040 \\ & (4.6) \\ & \hline \end{aligned}$ | $\begin{gathered} \hline 761.8- \\ 911.4 \\ \hline \end{gathered}$ | $\begin{gathered} 47.9- \\ 60.6 \\ \hline \end{gathered}$ | 59.8-73.0 |
| ID | $\begin{aligned} & 84,560 \\ & (70.9) \end{aligned}$ | $\begin{gathered} 21,952 \\ (18.3) \end{gathered}$ | $\begin{aligned} & 13,440 \\ & (11.2) \end{aligned}$ | $\begin{gathered} 469.6- \\ 493.6 \end{gathered}$ | $\begin{aligned} & 97.9- \\ & 110.1 \end{aligned}$ | $\begin{gathered} 134.6- \\ 134.9 \\ \hline \end{gathered}$ |
| MT | $\begin{gathered} 117,392 \\ (82.3) \end{gathered}$ | $\begin{gathered} 13,968 \\ (9.8) \\ \hline \end{gathered}$ | $\begin{gathered} 11,120 \\ (7.8) \end{gathered}$ | $\begin{gathered} 778.1 \text { - } \\ 813.6 \end{gathered}$ | $\begin{gathered} 60.8-70 \\ 2 \\ \hline \end{gathered}$ | $\begin{gathered} 102.4- \\ 104.3 \end{gathered}$ |
| WY | $\begin{aligned} & 66,064 \\ & (96.1) \end{aligned}$ | $\begin{aligned} & 1,936 \\ & (2.8) \end{aligned}$ | $\begin{aligned} & 720 \\ & (1.0) \end{aligned}$ | $\begin{gathered} 272.7- \\ 303.4 \end{gathered}$ | 7.2-8.8 | 4.4-5.9 |
| CO | $\begin{gathered} 124,160 \\ (94.5) \\ \hline \end{gathered}$ | $\begin{gathered} 6,048 \\ (46.2) \end{gathered}$ | $\begin{gathered} 688 \\ (0.5) \\ \hline \end{gathered}$ | $\begin{gathered} 173.9- \\ 370.5 \end{gathered}$ | $\begin{gathered} 21.2- \\ 26.5 \\ \hline \end{gathered}$ | 2.1-4.5 |
| UT | $\begin{aligned} & 92,528 \\ & (91.4) \end{aligned}$ | $\begin{aligned} & 8,496 \\ & (8.4) \\ & \hline \end{aligned}$ | $\begin{gathered} 224 \\ (0.2) \end{gathered}$ | $\begin{gathered} 105.6- \\ 145.4 \end{gathered}$ | $\begin{gathered} 29.6- \\ 32.5 \end{gathered}$ | 1.7-2.0 |
| NV | $\begin{aligned} & 61,104 \\ & (98.7) \\ & \hline \end{aligned}$ | $\begin{array}{r} 608 \\ (0.9) \\ \hline \end{array}$ | $\begin{gathered} 192 \\ (0.3) \\ \hline \end{gathered}$ | $\begin{gathered} 69.0- \\ 56.0 \end{gathered}$ | 1.9-2.0 | 2.2-5.7 |
| AZ | $\begin{aligned} & 99,088 \\ & (98.7) \\ & \hline \end{aligned}$ | $\begin{gathered} 1,232 \\ (1.2) \\ \hline \end{gathered}$ | $\begin{gathered} 96 \\ (0.1) \\ \hline \end{gathered}$ | $\begin{gathered} \hline-0.9- \\ 97.9 \end{gathered}$ | 3.9-4.7 | 0.6-0.8 |
| NM | $\begin{aligned} & 95,600 \\ & (98.6) \end{aligned}$ | $\begin{gathered} 1,200 \\ (1.2) \end{gathered}$ | $\begin{gathered} 160 \\ (0.2) \end{gathered}$ | $\begin{gathered} \hline-74.4- \\ 230.6 \end{gathered}$ | 4.2-6.1 | 1.1-1.4 |

## References

1. Buotte PC, et al. (2018) Near-future forest vulnerability to drought and fire varies cross the western US. Global Change Biology Online DOI:10.1111/gcb. 14490.
