

Geophysical Research Letters

RESEARCH LETTER

10.1029/2019GL082762

Key Points:

- Models using plant functional types or plant functional traits at large spatial scales lead to erroneous biome responses under changing climate
- Species-specific model parameterization more accurately captures individual species responses, a key tool to optimize forest management strategies
- Databases of species-specific physiologic traits for parameterization should help to improve ecosystem model projections under future climate

Supporting Information:

- Supporting Information S1

Correspondence to:

M. D. Hurteau,
mhurteau@unm.edu

Citation:

Remy, C. C., Krofcheck, D. J., Keyser, A. R., Litvak, M. E., Collins, S. L., & Hurteau, M. D. (2019). Integrating species-specific information in models improves regional projections under climate change. *Geophysical Research Letters*, 46, 6554–6562. <https://doi.org/10.1029/2019GL082762>

Received 8 MAR 2019

Accepted 25 MAY 2019

Accepted article online 4 JUN 2019

Published online 19 JUN 2019

Integrating Species-Specific Information in Models Improves Regional Projections Under Climate Change

Cécile C. Remy¹ , Dan J. Krofcheck¹, Alisa R. Keyser¹ , Marcy E. Litvak¹ , Scott L. Collins¹, and Matthew D. Hurteau¹ 

¹Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA

Abstract Models commonly used to project forest carbon response to climate change reduce biodiversity to a small number of plant functional types or plant functional traits for the sake of computational efficiency at large spatial scales. We simulated the climate sensitivity of the dominant woody vegetation types in New Mexico using both a generalized functional type and a species-specific model parameterization. Both parameterizations achieve reasonable current carbon uptake rates and aboveground biomass amount at the ecosystem scale. When vegetation types are subjected to increasing temperature and decreasing precipitation, the generalized parameterization differs substantially from the species-specific parameterization by homogenizing the diversity of adaptations for dealing with higher temperature and drought, leading to divergent responses under changing climate. We recommend integrating species-specific information, when available, to improve projections of climate change impacts on forested ecosystems to develop robust ecosystem management strategies at regional scales.

Plain Language Summary Vegetation responses to climate change are commonly simulated using models that generalize the characteristics of species and ecosystems to facilitate global-scale modeling efforts. We compared the climate sensitivity of the dominant woody vegetation types in New Mexico using a simplified model parameterization that treated all species the same, regardless of ecosystem type, versus a species-specific model parameterization. Our results show that a simplified model parameterization can achieve reasonable current carbon uptake rates at the ecosystem scale. However, when subjected to increasing temperature and decreasing precipitation, the generalized parameterization differs substantially from the species-specific parameterization by homogenizing the diversity of adaptations for dealing with higher temperature and drought. We recommend integrating species-specific information, when available, to facilitate the development of ecosystem management strategies because management decisions focus on the biology of the species that comprise ecosystems.

1. Introduction

Accelerated tree-mortality driven by hotter droughts threatens forests and their contribution to regulating the climate system through carbon uptake and storage (Adams et al., 2009; Allen et al., 2015; Frank et al., 2015; Heimann & Reichstein, 2008; Williams et al., 2013). Many projections of forest carbon response to climate change are based on models that simplify tree species diversity by defining vegetation characteristics as functional traits (Purves & Pacala, 2008; Yang et al., 2015). However, it is broadly accepted that individual species respond uniquely to abiotic and biotic factors (Chen et al., 2011; Liu et al., 2018; Pearson & Dawson, 2003; Plaut et al., 2012; Walther, 2010). Quantifying the influence of species-specific responses to climate change is central to developing robust forest projections of carbon dynamics and management strategies.

Empirical studies of terrestrial ecosystem responses to climate change have documented widespread evidence of species-specific range expansion, contraction, and extinction (Neilson et al., 2005; Pecl et al., 2017). However, the Dynamic Global Vegetation Models (DGVM) commonly used to simulate terrestrial ecosystems at a global scale reduce biodiversity to a small number of plant functional types (PFT) or functional traits (FT) for the sake of computational efficiency (Fischer et al., 2015; Pavlick et al., 2013; Yang et al., 2015).

Two major disadvantages emerge from simplifying forests to functional types or assemblages of traits. First, the taxonomic unit of both legal environmental frameworks (e.g. US Endangered Species Act) and

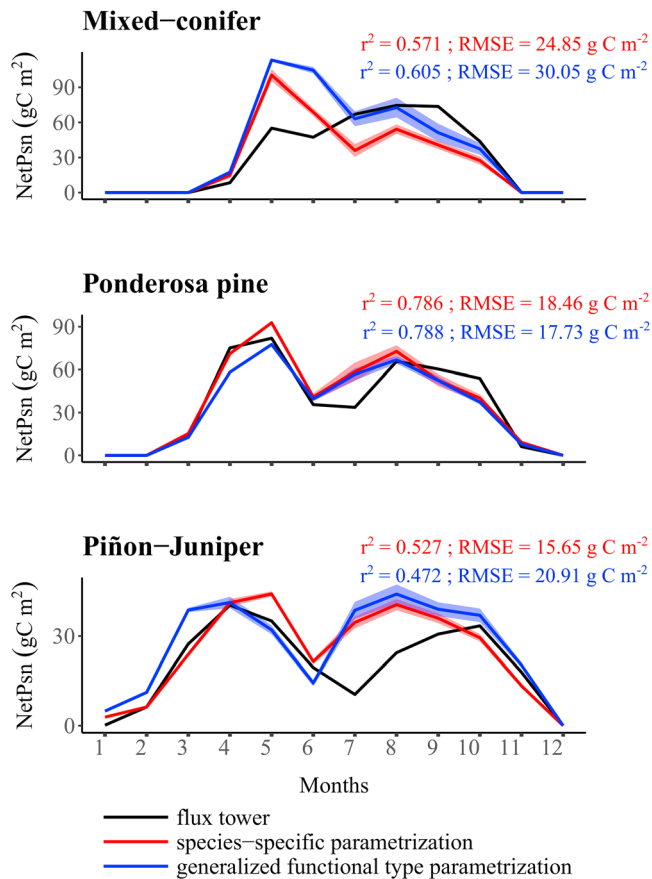


Figure 1. Averages of simulated monthly net photosynthesis (net Psn) from the species-specific parameterization (red) and the generalized functional type parameterization (blue) for three New Mexico sites with eddy-covariance observations (black). Shading represents the standard error and is computed from January 2007 to December 2012 for the mixed-conifer site, from January 2007 to December 2016 for the ponderosa pine site, and from January 2008 to December 2016 for the piñon-juniper site for the flux towers and from the 30 replicate simulations at each site for the two different model parameterizations. For the mixed-conifer site, data from January 2013 to December 2017 were excluded because of carbon flux uncertainties due to stand-replacing wildfire.

management decision-making is the species. Forest ecosystem management strategies for a range of objectives, including habitat and ecosystem service provision, are in part dependent upon understanding how the species that comprise ecosystems will respond to global change factors (Gamfeldt et al., 2013; Lindenmayer et al., 2006). Second, even if a generalized representation of an ecosystem produces reasonable aggregate carbon dynamics under current climate, the results could be due to counteracting errors leading to a reasonable overall outcome. For example, in a mixed-species forest, overall carbon uptake may not change because growth in one species is compensating for declines in another (Hurteau et al., 2014). The direction and magnitude of different error sources may change with projected climate, yielding high uncertainty under projected changes in climate (Buotte et al., 2018; McDowell et al., 2015; McMahon et al., 2011; Purves & Pacala, 2008).

Arid and semi-arid ecosystems are especially vulnerable to climate warming and resultant drying due to increased atmospheric water demand (Allen et al., 2010; Breshears & Barnes, 1999). In the southwestern United States (US), hotter droughts and climate-driven increases in disturbance intensity are causing increased tree mortality and having disproportionate impacts on some tree species, with increased vulnerability to drought-mortality projected under future climate (Breshears et al., 2005; Buotte et al., 2018; Williams et al., 2010). For example, piñon-juniper woodlands, the most common woody vegetation type in the southwestern US, show differential drought-related mortality between species (Gaylord et al., 2013; Mueller et al., 2005). Yet, in a DGVM framework, all southwestern woody vegetation is represented by one biome type that aggregates the traits of evergreen needleleaf species (Lawrence & Chase, 2007; McDowell et al., 2015).

Given the empirical evidence of species-specific differences in response to changing climate, we sought to quantify the differences between a model parameterization that includes species-specific values and a generalized functional type parameterization on projected carbon dynamics and future vegetation trajectories. To achieve this objective, we simulated the climate sensitivity of the carbon dynamics for the dominant woody vegetation types in New Mexico, US to incremental changes in temperature and precipitation using both a generalized functional type and a species-specific model parameterization (Goeking et al., 2014).

2. Data and Methods

We conducted simulations for three sites from the New Mexico Elevation Gradient (NMEG) of eddy-covariance flux towers located in mixed-conifer forest, ponderosa pine forest, and piñon-juniper woodland (described in Anderson-Teixeira et al., 2011; Table S1). We used the LANDIS-II (v.6.0) forest landscape model with the PnET (Photosynthesis and EvapoTranspiration)-Succession mechanistic growth and succession extension (v.2.1.1) to simulate carbon fluxes and biomass pools of species-specific age-cohorts for the three ecosystem types (de Bruijn et al., 2014; Gustafson et al., 2015; Scheller et al., 2007). The PnET-Succession extension is based on the Biomass Succession extension of Scheller and Mladenoff (2004) and integrates the ecophysiology model PnET-II (Aber et al., 1995). The model is driven by monthly climate, photosynthetically active radiation, and atmospheric CO_2 data. We parameterized the model using tree inventory and soil data from the NMEG sites and species-specific ecophysiological characteristics from the literature (Table S2). We used US Forest Service Forest Inventory and Analysis data to develop age-diameter relationships to parameterize cohort ages (available at <https://www.fia.fs.fed.us/>). We used soil data from SSURGO datasets (Soil Survey Geographic Database, available at <https://websoilsurvey.nrcs.usda.gov/>). Tree inventory data from four 10 m radius circle plots at each site were also used to quantify the current

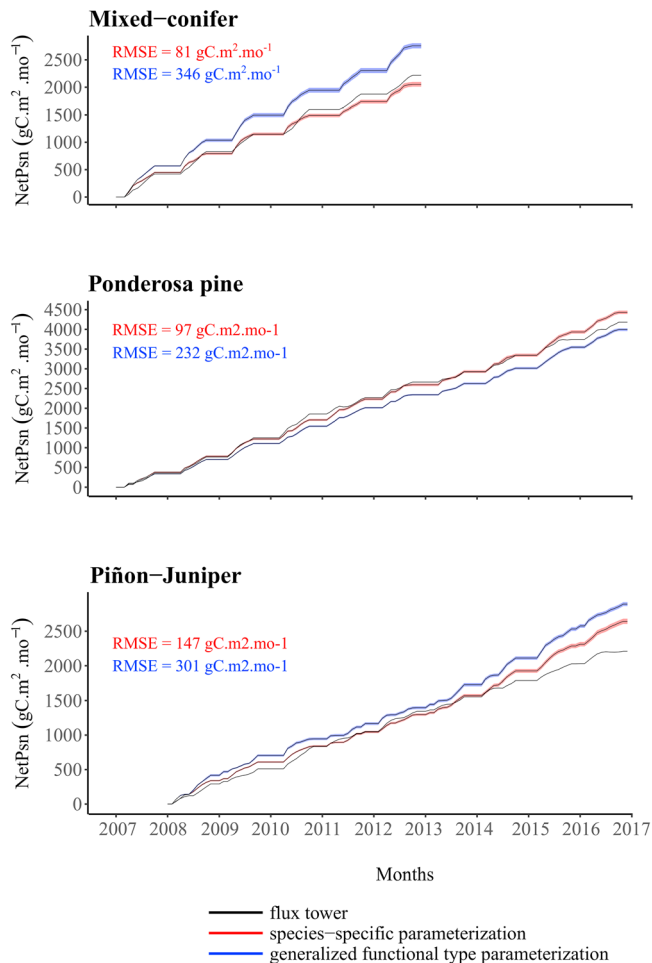


Figure 2. Simulated monthly cumulative net photosynthesis (NetPsn) from the species-specific and the generalized functional type parameterizations at the three sites and compared with eddy-covariance observations. The shaded envelopes correspond to the standard deviation around the mean from 30 replicate simulations. For the mixed-conifer site, data from January 2013 to December 2017 were excluded because of carbon flux uncertainties due to stand-replacing wildfire.

lected from four circular plots (10 m radius) at the three sites using a t-test. We then computed differences of simulated annual net photosynthesis from the two parameterizations under incremental increases in temperature and decreases in precipitation. To allow vegetation to stabilize under warmer and drier climates, we ran simulations for 200-years and took the mean of the last decade of each of the 30 replicate simulations to compare net photosynthesis.

3. Calibration and Validation of Species-Specific Parameterization

When compared to the eddy-covariance observations, both parameterizations captured the within year variability of observed monthly net photosynthesis at the mixed-conifer, ponderosa pine and piñon-juniper sites due to the bimodal precipitation distribution (Figures 1, S1 & S2). The model overestimated net photosynthesis during spring and underestimated it during fall at the mixed-conifer site. This may be driven by the fact that the model does not distribute snowmelt water over time as occurs at this 3000 m elevation site (Gustafson & Miranda, 2018). Consequently, all water stored in the snowpack is plant available when spring temperatures rise above freezing. Additionally, the precipitation measurements made at the tower sites do not account for belowground water transport or entirely capture the portion of precipitation that falls as snow. However, simulated cumulative net photosynthesis tracked tower-measured cumulative net

aboveground biomass (AGB) by using genus-specific allometric equations (Chojnacky et al., 2014; Jenkins et al., 2003). We used monthly temperature, precipitation, and photosynthetically active radiation data from January 2007 to December 2017 at the mixed-conifer and ponderosa pine sites and from January 2008 to December 2017 at piñon-juniper site. We used monthly CO_2 data from the Mauna Loa Observatory (available at the NOAA website: ftp://aftp.cmdl.noaa.gov/products/trends/co2/co2_mm_mlo.txt).

We calibrated species-specific ecophysiological parameters at each site by comparing simulated net photosynthesis to eddy-covariance tower data over the measurement period (data available at <https://fluxnet.fluxdata.org>, Table S2). Following model validation against the tower data, we averaged the species-specific parameter values for the evergreen needle-leaf species across the three NMEG sites to create a generalized functional type parameterization; this parameterization does not account for the presence of deciduous broadleaf species at the sites, which only account for a small fraction of the biomass.

We designed 36 different climate scenarios, replicating each 30 times, to test simulated forest response in terms of carbon dynamics to climate using both the species-specific and generalized functional type parameterizations. We sampled from monthly distributions of temperature and precipitation from each tower site to generate climate data for each of the 30 replicate simulations for each vegetation type, thereby retaining site-specific seasonal temperature and precipitation variability. We increased mean monthly temperature from current to $+5^\circ\text{C}$ using 1°C increments and reduced mean monthly precipitation from current to -25% using 5% increments. This approach was applied to each of the replicate climate data sets to retain monthly variability. All simulations were performed by using site-specific current climate conditions for the model spin-up period, the length of which was governed by the age of the oldest tree cohort.

To evaluate the performance of the species-specific and generalized functional type parameterizations, we used the r-squared values to compare the monthly simulated net photosynthesis with the eddy-covariance flux tower records (net ecosystem production) and compared the annual simulated aboveground biomass with empirical aboveground biomass data col-

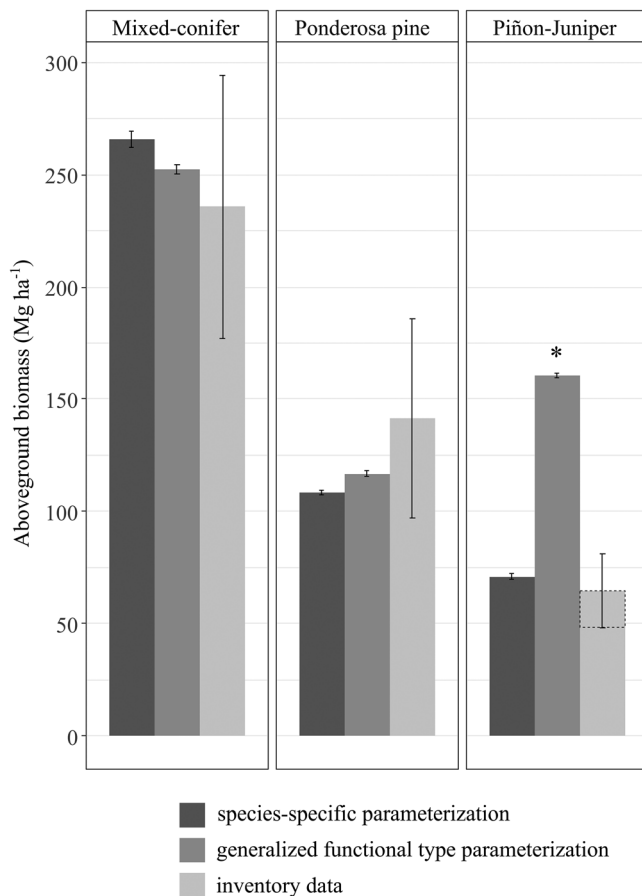


Figure 3. Mean of the aboveground biomass of woody vegetation types simulated with the species-specific and the generalized functional type parameterizations under current climate conditions, compared to empirical estimates from the inventory data at the flux tower sites. The dotted bar corresponds to the dead wood inventoried at the piñon-juniper site after a pine beetle outbreak that occurred from 2013 to 2016. Error bars correspond to the standard deviation computed from the 30 simulation replicates for both parameterizations, and from four circle plots at each flux tower site for the inventory data. An asterisk denotes when simulated aboveground biomass is significantly different ($p < 0.05$) from the empirical estimate.

photosynthesis well over the measurement period (Figure 2), indicating that there was little to no impact of these seasonal disparities on monthly fluxes over the course of the year.

4. Model Parameterization Comparison Under Current Climate

The simulated aboveground biomass (AGB) was within the range of variability for the empirical estimates for both parameterizations at the mixed-conifer site (Figure 3). The generalized parameterization had higher uptake during the growing season because of higher drought-resistance and more biomass allocated to root growth (Figure 1; Table S2), which resulted in reduced AGB relative to the species-specific parametrization results (Figure 3).

The generalized functional type parameterization performed similarly to the species-specific parameterization at the ponderosa pine site, which resulted in similar aboveground biomass estimates (Figures 1 & 3). However, the homogenization of parameter values resulted in ponderosa pine having a higher wilting point for photosynthesis, higher foliar nitrogen content, higher resistance to water stress and a higher amount of woody biomass that has active xylem capable of supporting foliage favorable for higher uptake (Table S2). These parameter values that increase carbon uptake were offset by lower specific leaf weight, higher canopy light attenuation, lower half saturation light level for photosynthesis and a lower fraction of the amount of active woody biomass that is allocated to foliage per year.

The largest difference in net photosynthesis and AGB between the two parameterizations and with empirical estimates occurred at the piñon-juniper site. A pine beetle outbreak occurred at the site from 2013 to 2016, which killed 60% of the piñon pine. We did not simulate this insect outbreak, which was largely responsible for the $18 \pm 6 \text{ Mg ha}^{-1}$ of dead wood inventoried at the site in 2017. Accounting for the beetle-induced transition from live to dead by including the AGB in dead trees (Figure 3; total live and dead AGB: $65 \pm 17 \text{ Mg ha}^{-1}$) indicates that the species-specific parameterization ($70 \pm 2 \text{ Mg ha}^{-1}$) better approximated AGB accumulation at the piñon-juniper site (live aboveground biomass: $47 \pm 11 \text{ Mg ha}^{-1}$) than the generalized functional type parameterization ($112 \pm 2 \text{ Mg ha}^{-1}$)

(Table S3). The generalized parameterization values increased piñon pine (*Pinus edulis*) net photosynthesis compared to the species-specific parameterization values (Figure S4) and resulted in a higher fraction of biomass aboveground and a higher amount of woody biomass that has active xylem capable of supporting foliage (Table S2).

5. Model Parameterization Comparison Under Changing Climate

The differences in net uptake between the two parameterizations under different climate conditions at the end of the 200-year simulation period demonstrate how a simplified approach encompassing the different vegetation types in only one biome can yield large differences compared to a species-specific simulation approach (Figure 4). Allowing the simulations to run for 200 years compounded the differences between the two parametrizations and caused large discrepancies in carbon uptake at the mixed-conifer and the ponderosa pine sites under current climate conditions (Figures 4 & S4, upper left corner). The use of the generalized functional type parameterization showed higher productivity in mixed-conifer and lower productivity in ponderosa pine relative to the species-specific parameterization (Figure S4). For mixed-conifer, the generalized parameterization increased the half saturation light level for photosynthesis and the intercept of

Difference between parameterizations
(generalized functional type - species-specific)

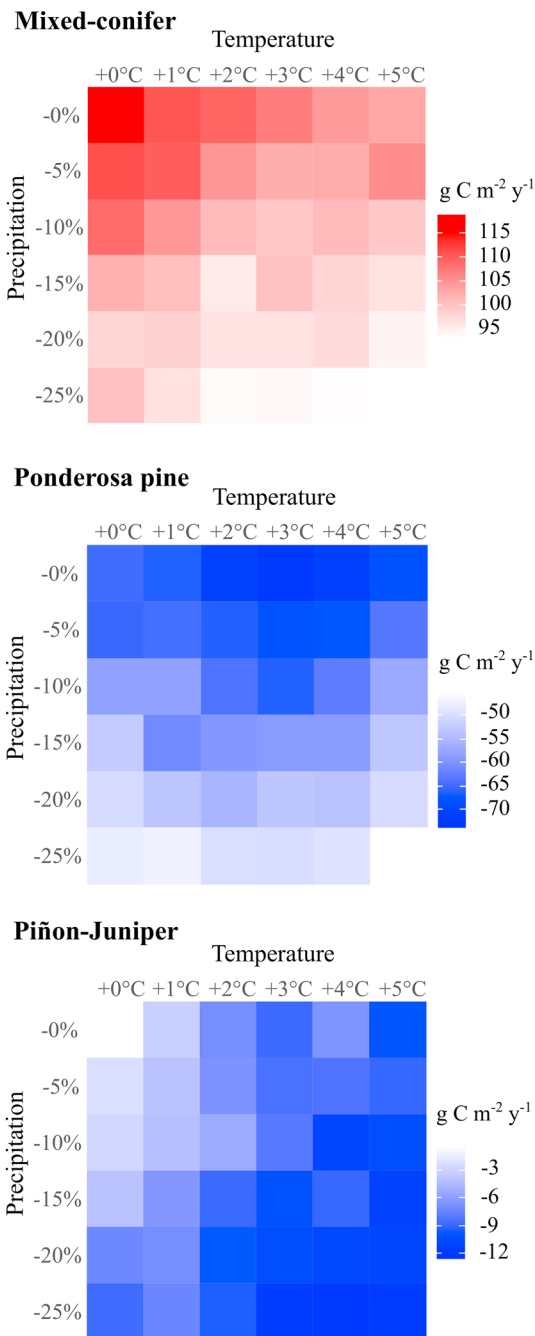


Figure 4. Difference between the annual net photosynthesis simulated with the generalized parameterization and with the species-specific parameterization at the three sites under different climate scenarios (see figure S2 for original simulated values from both parameterizations). Values correspond to the mean of the last decade of the 30 replicate 200-year simulations.

the relationship between foliar nitrogen content and maximum net photosynthetic rate of the coniferous species, leading to increased productivity. The lower productivity under the generalized parameterization in ponderosa pine is due to lower water use efficiency, lower half saturation light level for photosynthesis and lower maximum specific leaf weight for ponderosa pine (Figure 4 & Table S2). While the parameter differences were less apparent over the short time period of the flux tower record (Figure 1), they compounded when simulated over a longer time period. The general trends in mixed-conifer and ponderosa pine net photosynthesis were not linear for each incremental increase in temperature and decrease in precipitation (Figure 3). The mixed-conifer productivity increase and the ponderosa pine productivity decrease with the generalized parameterization was less pronounced under larger decreases in precipitation ($> -15\%$) because the low level of precipitation causes substantial drought-stress regardless of the drought sensitivity parameter values (Figure 4 & Table S2). The differences between the two parameterizations for piñon-juniper were less pronounced under lower amounts of warming and smaller decreases in precipitation (Figure 4). Piñon pine and juniper have distinct physiologies with respect to water use efficiency and water stress and the generalized parameterization is more similar to piñon (Table S2). As warming increased and precipitation decreased, the more piñon-like generalized parameterization (Figure 4) had larger declines in net photosynthesis than the species-specific parameterization because of the decreased water use efficiency (Figure S3 & Table S2). Under the species-specific parameterization, juniper is capable of continuing to take-up carbon under warmer and drier conditions (Figure S4). The difference between the two parameterizations for piñon-juniper is considerably lower than for mixed-conifer and ponderosa pine because piñon-juniper is a much less productive system.

6. Implications of Model Parameterization Choice at Biome Scale

On a per-unit area basis, the differences between the two model parameterizations are relatively small. However, in New Mexico, mixed-conifer forest (0.9 million ha), ponderosa pine forest (2 million ha), and piñon-juniper woodlands (5.3 million ha) cover 8.2 million hectares (USGS National Gap Analysis Program, 2005). If we assume that the productivity of each vegetation type is the same across the state, differences between the parameterizations compound substantially when scaled to the land area occupied by each vegetation type. For example, under current climate, the generalized parameterization ($24.7 \text{ Tg C yr}^{-1}$) carbon uptake is $0.24 \text{ Tg C yr}^{-1}$ lower than the species-specific parameterization uptake ($25.0 \text{ Tg C yr}^{-1}$) when scaled to the state-level (Table S4). Increasing temperature and decreasing precipitation exacerbated the differences between the two parameterizations when scaled to the state-level, with the generalized parameterization being lower by $0.32 \text{ Tg C yr}^{-1}$ (with a 10% decrease in precipitation and no increase in temperature) to $0.96 \text{ Tg C yr}^{-1}$ (with a 5°C increase in temperature and no decrease in precipitation).

These results demonstrate that while a simplified parameterization can achieve reasonable current carbon uptake rates at a biome-scale (Figures 1, 2 and 3), it is the result of counteracting errors within different

vegetation types. Consequently, these errors minimized or exaggerated the drought sensitivity of each vegetation type subjected to increasing temperature and decreasing precipitation (Figure 4). Most recent climate scenarios for the 21st century project that precipitation will decrease by 0–10% relative to the 1979–2005 average and temperature will increase by 1–2.5 °C by mid-century and 2.5–4.8 °C by late-century, relative to 1976–2005 within the southwestern US (USGCRP, 2017). At the site-scale, our simulations with mean temperature and precipitation values encompassing the latest projections show substantial differences between the generalized functional type and species-specific parameterizations (Figure 4). However, our results are solely based on model sensitivity to parameterization and climate.

Natural disturbances can act as a catalyst for vegetation change and some are projected to increase in frequency and severity with ongoing climate change (Bernhardt-Römermann et al., 2011; McDowell et al., 2015; Shellito & Sloan, 2006). Extreme drought, wildfire, and insect outbreaks are common in the southwestern US and can have significant implications for carbon dynamics (Allen et al., 2015; Bond et al., 2005; Hurteau, 2017; Williams et al., 2013; Turner, 2010). Extreme drought and insect outbreaks disproportionately affect some species (e.g. piñon *versus* juniper); a difference not captured by a simplified parameterization (Gaylord et al., 2013). Severe wildfire can act as a catalyst for biome change when dominant species are killed (Liang et al., 2017a). These disturbances are likely to shift the distribution of species and alter the composition of vegetation communities (Coop et al., 2016; Liang et al., 2017b), which could further compound the carbon uptake discrepancies that occur with the generalized parameterization under climate change (Buotte et al., 2018; Kolus et al., 2019).

Managing natural systems to meet societal objectives, including continued climate regulation, and quantifying the adaptive capacity of a particular ecosystem to ongoing climate change require understanding the responses of individual species that comprise the ecosystem. Plant competition, mortality, recruitment, and responses to disturbances are not well captured in generalized simulation approaches and the aggregate response of an ecosystem can be the result of compensatory effects between species (Hurteau et al., 2014; Moorcroft et al., 2006). Changes in the distribution of species and vegetation types could alter future fire and insect outbreak activity, depending on the species that establish following disturbance (Hicke et al., 2016; Thonicke et al., 2010). Managing to build adaptive capacity requires understanding the potential outcomes for different strategies and their ability to ameliorate the effects of host-specific insects and the effects of vegetation changes on fire hazard, among other disturbances (Hurteau, 2017; Scheller et al., 2018). Thus, a generalized functional type parameterization could lead to ill-informed decisions about adaptation and mitigation strategies for reducing the loss of woody biomass and carbon emissions (Kautz et al., 2018; Littell et al., 2011).

7. Conclusion and Perspectives

Our results demonstrate the importance of accounting for species-specific sensitivity to climate when simulating ecosystem carbon dynamics. Yet, adequately representing the diversity of species within ecosystem models will require a large number of species-specific parameter values and ecosystem-specific empirical data (e.g. net photosynthesis and aboveground biomass values); data that are limited in more diverse forest ecosystems (e.g. tropical ecosystems). Recent efforts to develop databases of ecophysiological parameters are advancing our ability to capture species-specific differences in ecosystem models (Kattge et al., 2012). Model validation data sets also face similar limitations, where the distribution of eddy-covariance measurements does not encompass the diversity of ecosystems (fluxnet.fluxdata.org). Moreover, eddy-covariance measurement density is correlated with measurement uncertainty and the regions of the globe most subject to rapid change are underrepresented in the empirical data (Schimel et al., 2015). Recent advances in remote sensing driven plant trait retrieval (Schneider et al., 2017) are helping to close these spatial knowledge gaps, and their inclusion in earth system models is being used to constrain uncertainty in global efforts (Butler et al., 2017).

Given the limitations inherent in the use of DGVMs based on plant functional types and functional traits to account for species-specific responses to climate change and the need for this information to develop robust ecosystem management strategies, integrating species-specific information in models and validation against ecosystem-specific empirical data should be a priority for improving projections of climate change impacts on forest and woodland ecosystems at regional scales.

Data

Simulation output data and code used in this study are available at https://digitalrepository.unm.edu/bio_data/2/.

Acknowledgments

This work is supported by the Interagency Carbon Cycle Science program grant no. 2017-67004-26486/project accession no. 1012226 from the USDA National Institute of Food and Agriculture and the Joint Fire Science Program under Project JFSP 16-1-05-8.

References

- Abel, J., Ollinger, S., Federer, C., Reich, P., Goulden, G., Kicklighter, D., et al. (1995). Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research*, 5(3), 207–222. <https://doi.org/10.3354/cr005207>
- Adams, H. D., Guardiola-Claramonte, M., Barron-Gafford, G. A., Villegas, J. C., Breshears, D. D., Zou, C. B., et al. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*, 106(17), 7063–7066. <https://doi.org/10.1073/pnas.0901438106>
- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), art129. <https://doi.org/10.1890/ES15-00203.1>
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, 259(4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Anderson-Teixeira, K. J., Delong, J. P., Fox, A. M., Brese, D. A., & Litvak, M. E. (2011). Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico. *Global Change Biology*, 17(1), 410–424. <https://doi.org/10.1111/j.1365-2486.2010.02269.x>
- Bernhardt-Römermann, M., Gray, A., Vanbergen, A. J., Bergès, L., Böhner, A., Brooker, R. W., et al. (2011). Functional traits and local environment predict vegetation responses to disturbance: A pan-European multi-site experiment. *Journal of Ecology*, 99(3), 777–787. <https://doi.org/10.1111/j.1365-2745.2011.01794.x>
- Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, 165(2), 525–538. <https://doi.org/10.1111/j.1469-8137.2004.01252.x>
- Breshears, D. D., & Barnes, F. J. (1999). Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: A unified conceptual model. *Landscape Ecology*, 14(5), 465–478. <https://doi.org/10.1023/A:1008040327508>
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., et al. (2005). Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences*, 102(42), 15,144–15,148. <https://doi.org/10.1073/pnas.0505734102>
- Buotte, P. C., Levis, S., Law, B. E., Hudiburg, T. W., Rupp, D. E., & Kent, J. J. (2018). Near-future forest vulnerability to drought and fire varies across the western United States. *Global Change Biology*, 25(1), 290–303. <https://doi.org/10.1111/gcb.14490>
- Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., et al. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences*, 114(51), E10937–E10946. <https://doi.org/10.1073/pnas.1708984114>
- Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024–1026. <https://doi.org/10.1126/science.1206432>
- Chojnacki, D. C., Heath, L. S., & Jenkins, J. C. (2014). Updated generalized biomass equations for North American tree species. *Forestry: An International Journal of Forest Research*, 87(1), 129–151. <https://doi.org/10.1093/forestry/cpt053>
- Coop, J. D., Parks, S. A., McClernan, S. R., & Holsinger, L. M. (2016). Influences of prior wildfires on vegetation response to subsequent fire in a burned southwestern landscape. *Ecological Applications*, 26(2), 346–354. <https://doi.org/10.1890/15-0775>
- de Bruijn, A., Gustafson, E. J., Sturtevant, B. R., Foster, J. R., Miranda, B. R., Lichti, N. I., & Jacobs, D. F. (2014). Toward more robust projections of forest landscape dynamics under novel environmental conditions: Embedding PnET within LANDIS-II. *Ecological Modelling*, 287, 44–57. <https://doi.org/10.1016/j.ecolmodel.2014.05.004>
- Fischer, R., Ensslin, A., Rutten, G., Fischer, M., Schellenberger Costa, D., Kleyer, M., et al. (2015). Simulating carbon stocks and fluxes of an African tropical montane forest with an individual-based forest model. *PLoS ONE*, 10(4), e0123300. <https://doi.org/10.1371/journal.pone.0123300>
- Frank, D., Reichstein, M., Bahn, M., Thonicke, K., Frank, D., Mahecha, M. D., et al. (2015). Effects of climate extremes on the terrestrial carbon cycle: Concepts, processes and potential future impacts. *Global Change Biology*, 21(8), 2861–2880. <https://doi.org/10.1111/gcb.12916>
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., et al. (2013). Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications*, 4(1), 1340. <https://doi.org/10.1038/ncomms2328>
- Gaylord, M. L., Kolb, T. E., Pockman, W. T., Plaut, J. A., Yezpez, E. A., Macalady, A. K., et al. (2013). Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytologist*, 198(2), 567–578. <https://doi.org/10.1111/nph.12174>
- Goeking, S. A., Shaw, J. D., Witt, C., Thompson, M. T., Werstak, C. E., Amacher, M. C., et al. (2014). New Mexico's forest resources, 2008–2012. *Resour. Bull. RMRS-RB-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station*, 144 P., 18. <https://doi.org/10.2737/RMRS-RB-18>
- Gustafson, E. J., Bruijn, A. M. G. D., Pangle, R. E., Limousin, J.-M., McDowell, N. G., Pockman, W. T., et al. (2015). Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change. *Global Change Biology*, 21(2), 843–856. <https://doi.org/10.1111/gcb.12713>
- Gustafson, E. J., & Miranda, B. R. (2018). PnET-Succession v3.1 Extension user guide (p. 68). Northern Research Station: US Forest Service. Retrieved from <https://docs.google.com/viewer?a=v&pid=sites&srcid=ZGVmYXVxSdGRvWFpbnXpYVW5kaXNt2RlBHXneDo0ZGEwMjAyNDkzNzJiYzlj>
- Heimann, M., & Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature*, 451(7176), 289–292. <https://doi.org/10.1038/nature06591>
- Hicke, J. A., Meddens, A. J. H., & Kolden, C. A. (2016). Recent tree mortality in the Western United States from bark beetles and forest fires. *Forest Science*, 62(2), 141–153. <https://doi.org/10.5849/forsci.15-086>
- Hurteau, M. D. (2017). Quantifying the carbon balance of forest restoration and wildfire under projected climate in the fire-prone southwestern US. *PLoS ONE*, 12(1), e0169275. <https://doi.org/10.1371/journal.pone.0169275>

- Hurteau, M. D., Robards, T. A., Stevens, D., Saah, D., North, M., & Koch, G. W. (2014). Modeling climate and fuel reduction impacts on mixed-conifer forest carbon stocks in the Sierra Nevada, California. *Forest Ecology and Management*, 315, 30–42. <https://doi.org/10.1016/j.foreco.2013.12.012>
- Jenkins, J. C., Chojnacky, D. C., Heath, L. S., & Birdsey, R. A. (2003). National-scale biomass estimators for United States tree species. *Forest Science*, 49(1), 12–35. <https://doi.org/10.1093/forestscience/49.1.12>
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., et al. (2012). TRY - a global database of plant traits. *Global Change Biology*, 17(9), 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Kautz, M., Anthoni, P., Meddens, A. J. H., Pugh, T. A. M., & Arneth, A. (2018). Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States. *Global Change Biology*, 24(5), 2079–2092. <https://doi.org/10.1111/gcb.13974>
- Kolus, H. R., Huntzinger, D. N., Schwalm, C. R., Fisher, J. B., McKay, N., Fang, Y., et al. (2019). Land carbon models underestimate the severity and duration of drought's impact on plant productivity. *Scientific Reports*, 9(1), 2758. <https://doi.org/10.1038/s41598-019-39373-1>
- Lawrence, P. J., & Chase, T. N. (2007). Representing a new MODIS consistent land surface in the community land model (CLM 3.0). *Journal of Geophysical Research*, 112, G01023. <https://doi.org/10.1029/2006JG000168>
- Liang, S., Hurteau, M. D., & Westerling, A. L. (2017a). Response of Sierra Nevada forests to projected climate–wildfire interactions. *Global Change Biology*, 23(5), 2016–2030. <https://doi.org/10.1111/gcb.13544>
- Liang, S., Hurteau, M. D., & Westerling, A. L. (2017b). Potential decline in carbon carrying capacity under projected climate-wildfire interactions in the Sierra Nevada. *Scientific Reports*, 7(1), 2420. <https://doi.org/10.1038/s41598-017-02686-0>
- Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, 131(3), 433–445. <https://doi.org/10.1016/j.biocon.2006.02.019>
- Littell, J. S., McKenzie, D., Kerns, B. K., Cushman, S., & Shaw, C. G. (2011). Managing uncertainty in climate-driven ecological models to inform adaptation to climate change. *Ecosphere*, 2(9), art102. <https://doi.org/10.1890/ES11-00114.1>
- Liu, D., Peñuelas, J., Ogaya, R., Estiarte, M., Tielbörger, K., Slowik, F., et al. (2018). Species selection under long-term experimental warming and drought explained by climatic distributions. *New Phytologist*, 217(4), 1494–1506. <https://doi.org/10.1111/nph.14925>
- McDowell, N. G., Williams, A. P., Xu, C., Pockman, W. T., Dickman, L. T., Sevanto, S., et al. (2015). Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nature Climate Change*, 6(3), 295–300. <https://doi.org/10.1038/nclimate2873>
- McMahon, S. M., Harrison, S. P., Armbruster, W. S., Bartlein, P. J., Beale, C. M., Edwards, M. E., et al. (2011). Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology & Evolution*, 26(5), 249–259. <https://doi.org/10.1016/j.tree.2011.02.012>
- Moorcroft, P. R., Pacala, S. W., & Lewis, M. A. (2006). Potential role of natural enemies during tree range expansions following climate change. *Journal of Theoretical Biology*, 241(3), 601–616. <https://doi.org/10.1016/j.jtbi.2005.12.019>
- Mueller, R. C., Scudder, C. M., Porter, M. E., Tablot Trotter, R. III, Gehring, C. A., & Whitham, T. G. (2005). Differential tree mortality in response to severe drought: Evidence for long-term vegetation shifts. *Journal of Ecology*, 93(6), 1085–1093. <https://doi.org/10.1111/j.1365-2745.2005.01042.x>
- Neilson, R. P., Pitelka, L. F., Solomon, A. M., Nathan, R., Midgley, G. F., Fragoso, J. M. V., et al. (2005). Forecasting regional to global plant migration in response to climate change. *Bioscience*, 55(9), 749–759. [https://doi.org/10.1641/0006-3568\(2005\)055\[0749:FRTGPM\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0749:FRTGPM]2.0.CO;2)
- Pavlick, R., Drewry, D. T., Bohn, K., Reu, B., & Kleidon, A. (2013). The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences*, 10, 4137–4177. <https://doi.org/10.5194/bg-10-4137-2013>
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12(5), 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Pech, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., et al. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214. <https://doi.org/10.1126/science.aai9214>
- Plaut, J. A., Yepez, E. A., Hill, J., Pangle, R., Sperry, J. S., Pockman, W. T., & McDowell, N. G. (2012). Hydraulic limits preceding mortality in a piñon-juniper woodland under experimental drought: Hydraulic limits in a piñon-juniper woodland. *Plant, Cell & Environment*, 35(9), 1601–1617. <https://doi.org/10.1111/j.1365-3040.2012.02512.x>
- Purves, D., & Pacala, S. (2008). Predictive models of forest dynamics. *Science*, 320(5882), 1452–1453. <https://doi.org/10.1126/science.1155359>
- Scheller, R. M., Domingo, J. B., Sturtevant, B. R., Williams, J. S., Rudy, A., Gustafson, E. J., & Mladenoff, D. J. (2007). Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling*, 201(3–4), 409–419. <https://doi.org/10.1016/j.ecolmodel.2006.10.009>
- Scheller, R. M., Kretschun, A. M., Loudermilk, E. L., Hurteau, M. D., Weisberg, P. J., & Skinner, C. (2018). Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the Lake Tahoe Basin. *Ecosystems*, 21(4), 643–656. <https://doi.org/10.1007/s10021-017-0175-3>
- Scheller, R. M., & Mladenoff, D. J. (2004). A forest growth and biomass module for a landscape simulation model, LANDIS: Design, validation, and application. *Ecological Modelling*, 180(1), 211–229. <https://doi.org/10.1016/j.ecolmodel.2004.01.022>
- Schimel, D., Pavlick, R., Fisher, J. B., Asner, G. P., Saatchi, S., Townsend, P., et al. (2015). Observing terrestrial ecosystems and the carbon cycle from space. *Global Change Biology*, 21(5), 1762–1776. <https://doi.org/10.1111/gcb.12822>
- Schneider, F. D., Morsdorf, F., Schmid, B., Petchey, O. L., Hueni, A., Schimel, D. S., & Schaepman, M. E. (2017). Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature Communications*, 8(1), 1441. <https://doi.org/10.1038/s41467-017-01530-3>
- Shellito, C. J., & Sloan, L. C. (2006). Reconstructing a lost Eocene paradise, part II: On the utility of dynamic global vegetation models in pre-quaternary climate studies. *Global and Planetary Change*, 50(1–2), 18–32. <https://doi.org/10.1016/j.gloplacha.2005.08.002>
- Thonicke, K., Spessa, A., Prentice, I. C., Harrison, S. P., Dong, L., & Carmona-Moreno, C. (2010). The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: Results from a process-based model. *Biogeosciences*, 7(6), 1991–2011. <https://doi.org/10.5194/bg-7-1991-2010>
- Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, 91(10), 2833–2849. <https://doi.org/10.1890/10-0097.1>
- USGS National Gap Analysis Program (2005). Southwest regional GAP analysis project—land cover descriptions. RS/GIS Laboratory, College of Natural Resources, Utah State University.

- Walther, G.-R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 365(1549), 2019–2024. <https://doi.org/10.1098/rstb.2010.0021>
- Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., et al. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, 3(3), 292–297. <https://doi.org/10.1038/nclimate1693>
- Williams, A. P., Allen, C. D., Millar, C. I., Swetnam, T. W., Michaelsen, J., Still, C. J., & Leavitt, S. W. (2010). Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences*, 107(50), 21,289–21,294. <https://doi.org/10.1073/pnas.0914211107>
- Yang, Y., Zhu, Q., Peng, C., Wang, H., & Chen, H. (2015). From plant functional types to plant functional traits: A new paradigm in modelling global vegetation dynamics. *Progress in Physical Geography: Earth and Environment*, 39(4), 514–535. <https://doi.org/10.1177/0309133315582018>

References From the Supporting Information

- Arthur, M. A., & Fahey, T. J. (1992). Biomass and nutrients in an Engelmann spruce–subalpine fir forest in north Central Colorado: Pools, annual production, and internal cycling. *Canadian Journal of Forest Research*, 22(3), 315–325. <https://doi.org/10.1139/x92-041>
- Clary, W. P., & Tiedemann, A. R. (1986). Distribution of biomass within small tree and shrub form *Quercus gambelii* stands. *Forest Science*, 32(1), 234–242. <https://doi.org/10.1093/forestscience/32.1.234>
- Duveneck, M. J., & Thimpson, J. R. (2017). Climate change imposes phenological trade-offs on forest net primary productivity. *Journal of Geophysical Research: Biogeosciences*, 122, 2298–2313. <https://doi.org/10.1002/2017JG004025>
- Gulke, N. E., & Retzlaff, W. A. (2001). Changes in physiological attributes of ponderosa pine from seedling to mature tree. *Tree Physiology*, 21(5), 275–286. <https://doi.org/10.1093/treephys/21.5.275>
- Keyes, M. R., & Grier, C. C. (1981). Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Canadian Journal of Forest Research*, 11(3), 599–605. <https://doi.org/10.1139/x81-082>
- Kolb, T. E., & Stone, J. E. (2000). Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine–oak forest. *Tree Physiology*, 20(1), 1–12. <https://doi.org/10.1093/treephys/20.1.1>
- Massman, W. J. (2000). A simple method for estimating frequency response corrections for eddy covariance systems. *Agricultural and Forest Meteorology*, 104(3), 185–198. [https://doi.org/10.1016/S0168-1923\(00\)00164-7](https://doi.org/10.1016/S0168-1923(00)00164-7)
- McKinnon, L. M., & Mitchell, A. K. (2003). Photoprotection, not increased growth, characterizes the response of Engelmann spruce (*Picea engelmannii*) seedlings to high light, even when resources are plentiful. *New Phytologist*, 160(1), 69–79. <https://doi.org/10.1046/j.1469-8137.2003.00854.x>
- Scott, K. I., & Benjamin, M. T. (2003). Development of a biogenic volatile organic compound emission inventory for the SCOS97-NARSTO domain. Appendix B: Development of a biogenic hydrocarbon emission inventory for the Central California ozone study domain. *Atmospheric Environment*, 37(2), 39–49. [https://doi.org/10.1016/S1352-2310\(03\)00381-9](https://doi.org/10.1016/S1352-2310(03)00381-9)
- Simonin, K. A. (2000). *Quercus gambelii*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Retrieved from <https://www.fs.fed.us/database/feis/plants/tree/quefgam/all.html> (2018, June 26).
- Tinus, R. W., Bourque, J. E., & Wallner, S. J. (1985). Estimation of cold hardiness of Douglas-fir and Engelmann spruce seedlings by differential thermal analysis of buds. *Annals of Applied Biology*, 106(2), 393–397. <https://doi.org/10.1111/j.1744-7348.1985.tb03129.x>
- Van Aiken, O. W., & Bush, J. K. (2017). Succession in *Quercus gambelii* (Gambel's oak) woodlands. *American Journal of Plant Sciences*, 08(02), 96–112. <https://doi.org/10.4236/ajps.2017.82008>
- Wang, J. R., Letchford, T., Comeau, P., & Kimmins, J.-P. (2000). Above- and below-ground biomass and nutrient distribution of a paper birch and subalpine fir mixed-species stand in the sub-boreal spruce zone of British Columbia. *Forest Ecology and Management*, 130(1–3), 17–26. [https://doi.org/10.1016/S0378-1127\(99\)00193-0](https://doi.org/10.1016/S0378-1127(99)00193-0)
- Webb, E. K., Pearman, G. I., & Leuning, R. (1980). Correction of flux measurements for density effects due to heat and water vapour transfer. *Quarterly Journal of the Royal Meteorological Society*, 106(447), 85–100. <https://doi.org/10.1002/qj.49710644707>
- Wennerberg, S. (2004). Plant Guide, White fire *Abies concolor* (Gord. & Glend.) Lindl. Ex. Hildebr. [Online]. U.S. Department of Agriculture, NRCS National Plant Data Center, Baton Rouge, Louisiana (Producer). Retrieved from https://plants.usda.gov/plantguide/pdf/pg_abco.pdf (2018, June 26).
- Zak, D. R., Pregitzer, K. S., Curtis, P. S., Vogel, C. S., Holmes, W. E., & Lussenhop, J. (2000). Atmospheric CO₂, soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecological Applications*, 10(1), 34–46. [https://doi.org/10.1890/1051-0761\(2000\)010\[0034:ACSNA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0034:ACSNA]2.0.CO;2)