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Integrating ecophysiology and forest landscape models to improve projections of drought effects under climate change

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Abstract

Fundamental drivers of ecosystem processes such as temperature and precipitation are rapidly changing and creating novel environmental conditions. Forest landscape models (FLM) are used by managers and policy-makers to make projections of future ecosystem dynamics under alternative management or policy options, but the links between the fundamental drivers and projected responses are weak and indirect, limiting their reliability for projecting the impacts of climate change. We developed and tested a relatively mechanistic method to simulate the effects of changing precipitation on species competition within the LANDIS-II FLM. Using data from a field precipitation manipulation experiment in a piñon pine (*Pinus edulis*) and juniper (*Juniperus monosperma*) ecosystem in New Mexico (USA), we calibrated our model to measurements from ambient control plots and tested predictions under the drought and irrigation treatments against empirical measurements. The model successfully predicted behavior of physiological variables under the treatments. Discrepancies between model output and empirical data occurred when the monthly time step of the model failed to capture the short-term dynamics of the ecosystem as recorded by instantaneous field measurements. We applied the model to heuristically assess the effect of alternative climate scenarios on the piñon–juniper ecosystem and found that warmer and drier climate reduced productivity and increased the risk of drought-induced mortality, especially for piñon. We concluded that the direct links between fundamental drivers and growth rates in our model hold great promise to improve our understanding of ecosystem processes under climate change and improve management decisions because of its greater reliance on first principles.

Keywords: climate change, competition for light, drought, forest landscape disturbance and succession model, LANDIS-II, Piñon–juniper ecosystem, PnET-Succession, tree mortality, water stress

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Introduction

Ecosystems and landscapes are shaped by a multitude of processes operating across a continuum of scales from cellular to global. For example, primary productivity requires photosynthesis, which can be dependent on both local soil water availability and atmospheric CO_2 concentration. Similarly, some disturbance processes, such as fire, are driven by both local fuel conditions (vegetation) and global climate patterns. Fundamental drivers of these processes, such as temperature, precipitation, and atmospheric CO_2 concentrations, are rapidly changing and creating novel environmental conditions that have not occurred during the scientific age (IPCC 2013).

Managers and policy-makers are charged with ensuring the viability of natural resources and ecosystem services into the future. They typically rely on projections of future ecosystem dynamics under alternative management or policy options to guide their decisions. Because ecosystems are so complex, with a great many interacting spatial and aspatial processes and drivers, simulation models are usually needed to make these predictions (e.g., Gustafson, 2013). These models can have both mechanistic and phenomenological components. Mechanistic components explicitly model the mechanisms by which causes produce effects within a process (De Bruijn *et al.*, 2011). Phenomenological (sometimes called empirical or statistical) components

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model system outcomes, where the causes of a process produce effects (phenomena) according to how the system has typically behaved in the past (Schelhaas *et al.*, 2004). Therefore, the effect of the process is predicted using surrogates for the mechanism, thus mimicking the effect of the mechanism on the system. However, given the accelerating pace of multiple global changes, it is becoming increasingly difficult to trust projections of the future made by phenomenological models estimated under the conditions of the past (Cuddington *et al.*, 2013; Gustafson, 2013). This difficulty persists even when empirical relationships have been estimated between fundamental drivers (e.g., temperature, precipitation) and system response, because the relationships under future conditions may need to be extrapolated beyond the domain of the empirical data (Keane *et al.*, in review).

The phenomenological approach may also be problematic when the interactions among phenomena are difficult to predict. Consider the effects of climate change on tree growth. Precipitation can increase, decrease or stay the same, depending on location. However, elevated temperature increases evapotranspiration, resulting in increased water stress even if precipitation remains unchanged from past patterns (Williams *et al.*, 2013). Furthermore, a change in temperature relative to the species optimal photosynthesis temperature may impact photosynthetic efficiency either positively or negatively. Respiration rates generally increase with temperature, reducing net photosynthesis and increasing the metabolic cost of tissue maintenance (Amthor, 1994; Atkin *et al.*, 2007). To further add to the complexity, elevated CO_2 can help sustain photosynthesis when water stress reduces stomatal conductance (Franks *et al.*, 2013).

Forest landscape models (FLM) have proven useful to predict ecosystem dynamics at landscape scales for various research and management applications (Scheller *et al.*, 2007; He, 2008). FLMs operate at scales between those of stand-level gap (e.g., SORTIE, Pacala *et al.*, 1993) and ecosystem physiology (e.g., PnET, Aber *et al.*, 1995) models, and biome-level Dynamic Global Vegetation Models (Medlyn *et al.*, 2011). FLMs generally have components that simulate successional change and various disturbances. They were initially developed to explore various management and/or disturbance scenarios, but they have recently been used to investigate how climate change may impact future landscape dynamics (Swanston *et al.*, 2011). Although most FLMs have a combination of mechanistic and phenomenological components, integration of climate drivers and their interacting effects across the process components of the models is challenging. Linking growth and competition to climate drivers has been particularly problematic (Gustafson, 2013; Keane *et al.*, in review). Even the most mechanistic FLMs do not have strong, direct links between climate state variables and establishment, growth or competition. This has made the simulation of drought impacts on forest landscape dynamics challenging. Gustafson & Sturtevant (2013) developed a phenomenological approach using empirical statistical models relating a drought index to the loss of tree biomass to drought-induced mortality in the upper Midwest (USA) in the recent past, but it is questionable whether these relationships can be extrapolated to future conditions because elevated CO_2 may have differential effects on photosynthetic efficiency (Drake *et al.*, 1997).

Although many system-level empirically derived relationships estimated in the past may have limited applicability under future conditions, this problem is less acute at the first principles levels of physiology and biophysics (Gustafson, 2013). A large body of empirical research has elucidated a number of relationships between fundamental drivers (water, temperature, and light) and the foundational processes of photosynthesis, growth and competition. Because these relationships were often derived for a wide range of driver values under field or laboratory conditions, their domain often includes the conditions expected in the future. Furthermore, because they are first principles relationships, they are the strongest mechanistic relationships available for a model.

Our purpose in this article was to develop and test a relatively mechanistic method to simulate the effects of drought within a FLM. We capitalized on a newly developed succession extension (PnET-Succession) for the LANDIS-II FLM that embedded the PnET-II ecophysiology model (Aber *et al.*, 1995) into an existing succession extension to mechanistically simulate growth as a competition for light and water to support photosynthesis (De Bruijn *et al.*, 2014). Because water and temperature are the fundamental drivers that determine net growth (carbon fixation minus respiration), water stress can result in a negative carbon balance and eventually, tree death. It was our expectation that this approach would reliably predict drought mortality and be robust to the novel environmental conditions expected in the future. Our specific objectives were to: (1) apply the PnET-Succession extension to explicitly link moisture stress to photosynthesis and the allocation and consumption of carbon reserves, (2) calibrate the extension in a piñon–juniper ecosystem and test its ability to predict the outcome of a precipitation manipulation experiment, (3) assess the ability of the model to predict growth reductions and mortality risk as a consequence of drought, and (4) use the new extension to study the long-term effects of changing climate (temperature, precipitation, and CO_2) in piñon–juniper ecosystems.

Materials and methods

LANDIS-II (Scheller *et al.*, 2007) simulates broad-scale (>10^5 ha) landscape dynamics over long (i.e., century-scale) temporal scales, including succession, multiple natural disturbance types, seed dispersal, forest management, and climate change effects. Landscapes are represented as a grid of interacting cells with user-defined cell size. Individual cells are assumed to have homogeneous canopy layering, and are spatially aggregated into land types with homogeneous climate and soils. Forest composition at the cell level is represented as age cohorts of individual tree species that interact via a suite of vital attributes (e.g., shade tolerance, fire tolerance, seed dispersal, ability to sprout vegetatively, and longevity) to produce nondeterministic successional pathways sensitive to disturbance type and severity (Mladenoff, 2004). LANDIS-II v6 consists of a core collection of libraries and a collection of optional extensions that represent the ecological processes of interest (Scheller & Domingo, 2012).

Aside from the simplest succession extension based on the original LANDIS model (Mladenoff *et al.*, 1996) and the most recent succession extension described here, prior succession extensions modeled aboveground competition among species and age cohorts for 'growing space' as a function of relative growth rates of species. In the Biomass Succession extension (Scheller & Mladenoff, 2004) for example, available growing space is calculated as potential biomass that a cell can support minus biomass already occupied by other species age cohorts. Maximum annual net primary production ($ANPP_{max}$) determines relative growth rates among species. Actual ANPP for a tree species age cohort is reduced by competition when the available growing space decreases. Soil water availability is not explicitly modeled. The $ANPP_{max}$ parameter is typically estimated to reflect mean climate and soil characteristics (or CO_2 concentration) for a specific ecoregion. $ANPP_{max}$ can be modified at the scale of the time step (typically 5–10 years), but growth rate does not vary within a time step (i.e., there is no variation analogous to weather).

Biomass Succession in LANDIS-II has been loosely coupled to ecophysiology models, which are used to estimate how growth rates (e.g., $ANPP_{max}$) will respond to changes in climate, providing a mean maximum growth rate for the climatic conditions of the model. However, extreme weather events such as drought can have a significant structuring effect on forests and impact their dynamics, but are poorly simulated using mean growth rates. Furthermore, the integration of climate and other fundamental drivers among the processes (growth, establishment, and disturbance) simulated within the model is weak. For example, a drought may not only depress growth rates but also establishment rates, even when a drought-enhanced fire has created available sites for establishment. Furthermore, drought stress may directly cause mortality by depressing productivity below respiration rates, or by increasing susceptibility to specific disturbances (e.g., insects). A tighter coupling of ecophysiology models with succession and disturbance extensions would help resolve these inconsistencies.

In the more mechanistic LANDIS-II succession modeling approach developed by De Bruijn *et al.* (2014) (PnET-Succession), the "growing space" algorithms of Biomass Succession (Scheller & Mladenoff, 2004) were replaced by algorithms from the ecophysiology model PnET-II (Aber *et al.*, 1995). PnET upscales small scale (i.e., per gram foliage) biochemical processes such as photosynthesis, respiration, and transpiration to the scale of a grid cell by integrating light extinction and water consumption in stacked canopy layers and computing a dynamic soil water balance. First, species-cohort growth rates are calculated as a function of photosynthesis, which depends fundamentally on light and soil water availability. Soil water is tracked at the grid-cell level using a bulk-hydrology model based on precipitation, loss to evaporation, runoff, and percolation out of the rooting zone, and consumption by species cohorts. Cohorts compete for water and light in each cell, and cohort age and biomass determines the priority of access to light and soil moisture, with the largest cohorts having first access to both resources. When water is adequate, the rate of photosynthesis (leaf area index) for a given species cohort increases with light that is available to the cohort (dependent on canopy position and leaf area), atmospheric CO_2 concentration and foliar N, and decreases with age and departure from optimal temperature. As soil water availability decreases, photosynthesis also decreases. PnET-Succession accounts for reductions in photosynthesis due to growth and maintenance respiration using a Q10 relationship (Atkins, 1978), such that foliar respiration rate depends on temperature and moisture, while maintenance respiration depends on temperature and biomass. Net photosynthetic production is allocated to biomass pools of foliage, wood, root, and reserves (nonstructural carbon) according to allocation parameters (RStRatio, dNSC, Table 1). Establishment of new cohorts is stochastic with species-specific probabilities calculated monthly as a function of soil water and subcanopy light.

Thus, in the PnET-Succession extension, photosynthetic rates (and therefore growth rates) vary monthly by species and cohorts as a function of precipitation and temperature (among other factors), which directly affects competition and ultimately successional outcomes. Capitalizing on this approach, drought-induced growth reductions result from water stress, and mortality can result if carbon reserves become depleted by respiration. Such mortality may be dependent on both the intensity and duration of water limitations, depending on the ability of a species to extract water from the soil and maintenance respiration rates. For studies of the effects of climate change on forest successional dynamics, a weather stream of temperature, precipitation, and radiation from downscaled global circulation models can allow growth and establishment rates to vary at each time step, and drought-induced mortality is simulated when moisture stress depresses growth rates below respiration levels long enough to reduce carbon reserves below survival thresholds.

Model calibration

To test the ability of the PnET-Succession extension to simulate the effects of drought (and higher precipitation) on tree growth and mortality, we applied the model to a field precipitation manipulation experiment at the Sevilleta Long Term

Table 1 Parameter values used in the simulations. Parameters that were varied for calibration are indicated by *

Parameter	Description	Parameter value		Source
Site variables				
Latitude	Latitude (degrees)	34N		Pangle *et al.* (2012)
WHC	Water Holding Capacity (mm)	162		Unpublished data
Water balance variables		Juniper	Piñon	
PrecLossFrac*	Fraction of precipitation not entering soil	0.5	0.5	Expert judgment
LeakageFrac	Fraction of precipitation percolating out of the root zone	0.06	0.06	Species arbitrarily the same
GrMstSens	Tuning parameter controlling ability of species to extract water from soil	0.3	0.3	Species arbitrarily the same
WltPnt	Fraction of WHC below which species is unable to take up water	0.05	0.05	Species arbitrarily the same
DVPD1	Coefficients for power function converting	0.05	0.05	Aber *et al.* (1995)
DVPD2	VPD to fractional loss in photosynthesis	2.0	2.0	Aber *et al.* (1995)
WUEConst*	Constant in equation for WUE as a function of VPD	30	28	Tuned
Canopy variables				
GDDFolStart	Growing degree days (base 4 °C) when foliage growth starts	200	200	Expert judgment
GDDFolEnd	Growing degree days (base 4 °C) when foliage growth ends	2000	2000	Expert judgment
TOfol	Fraction of foliage lost/year (reciprocal of leaf longevity)	0.167	0.167	Expert judgment
FolRet	Fraction of foliage C recovered prior to leaf drop	0.0	0.0	Expert judgment
SenescSt	Date at which leaf senescence begins (Julian date)	275	275	Senescence observations and climate records
k	Canopy light extinction coefficient (unitless)	0.58	0.58	Only one canopy layer
Photosynthesis variables				
FolN	Foliar nitrogen content (%)	1.06	1.21	Unpublished data
AmaxA*	Intercept (A) and slope (B) of relationship between foliar N	22.3	14.3	Tuned
AmaxB	and max. net photosynthetic rate (μmol CO_2 m^{-2} leaf s^{-1})	0.0	0.0	Constant
HalfSat	Half saturation light level (μmol m^{-2} s^{-1})	950	800	Unpublished data
BFolResp*	Foliar respiration as a fraction of max. photosynthetic rate (mo^{-1})	0.06	0.10	Tuned
PsnAgeRed	Tuning parameter controlling senescence mortality (respiration > productivity) (unitless)	3	3	Assumed longevity of ~800 year
Q10	Q_{10} value for foliar respiration (unitless)	2.2	1.7	Gass (2010)
PsnTMin	Minimum temperature for photosynthesis (°C)	0	0	Unpublished data
PsnTOpt	Optimum temperature for photosynthesis (°C)	25	25	Expert judgment
SLWmax	Specific leaf weight at the top of canopy (g/m^2)	490	242	Unpublished data
Carbon balance variables				
TOroot	Fraction of root biomass lost to damage or death (yr^{-1})	0.05	0.04	Expert judgment
TOwood	Fraction of wood biomass lost to damage or death (yr^{-1})	0.04	0.03	Expert judgment
MaintResp	Tissue maintenance respiration as a fraction of biomass (mo^{-1})	0.002	0.002	Expert judgment
dNSC*	Fraction of NSC allocated to structural biomass pools (mo^{-1})	0.09	0.08	Expert judgment/tuned
RStRatio	Ratio of the size of root to stem biomass pools	0.55	0.55	Expert judgment

Ecological Research (LTER) site at the Sevilleta National Wildlife Refuge in central New Mexico, USA (34°23 11″ N, 106°31 46″ W). Four treatments were applied to 1600 m^2 plots (40 m × 40 m), each with three replicates, in a piñon pine (*Pinus edulis*) and juniper (*Juniperus monosperma*) ecosystem (Pangle *et al.*, 2012). Treatments consisted of: (1) irrigation plots that received 19 mm of supplemental water 3–6 times per growing season, (2) drought plots that received 55% of ambient rainfall by use of plastic gutters to divert rain, (3) cover-control plots (inverted gutters) that received ambient precipitation but allowed determination of treatment infrastructure artifacts, and (4) ambient control plots. Extensive physiological, biological, and abiotic measurements were collected during the experiment, including mortality observations, which are detailed by Pangle *et al.* (2012), Plaut *et al.* (2012) and Limousin *et al.* (2013).

We simulated the years of the experiment (2007–2013) using PnET-Succession (v1) with a site (cell) size of 40 m, allowing simulation of an experimental plot with a single cell. PnET-Succession initializes species cohorts by simulating their growth from the year of establishment. The age of the trees on the experimental plots was unknown, but we assumed it was 200 years based on their size and a limited number of tree cores (A. Macalady, personal communication). For the period

1807–2007, we used average monthly temperature and precipitation from data collected at the Bosque del Apache weather station (located about 50 km south) between 1894 and 2005, and from 2007 onward we used weather data measured at the experiment site (Pangle *et al.*, 2012). We used a CO_2 concentration of 340 ppm prior to 2007 and CO_2 gradually rose from 386 in 2007 to 398 in 2013. We calibrated the model by comparing model output for the period 2007–2012 to empirical measures (water use efficiency, net photosynthesis, respiration, transpiration, and soil water) from the ambient control plots taken on specific dates during the growing seasons in 2010 and 2011 (Limousin *et al.*, 2013), and iteratively modified five tuning parameters (Table 1) to produce model behavior consistent (both in magnitude and temporal variation) with the empirical measurements. This period included a somewhat wet year (2010) and a drought year (2011), providing a range of conditions for calibration purposes.

We estimated mean soil water holding capacity from volumetric water content data from an ambient control plot, and calibrated the fraction of precipitation lost to evaporation and surface runoff to produce a soil water balance dynamic that varied similarly to empirical observations on the plot by tuning PrecLossFrac (see Table 1 for variable definitions) to a performance optima within reasonable values based on expert judgment. We assumed that percolation through the soil profile and out of the rooting zone was low because soils in this arid site are rarely saturated. Secondly, net photosynthesis rates were calibrated independently of foliar nitrogen concentration by setting AmaxB to zero and calibrating AmaxA to match empirical dynamics. Foliar respiration was calibrated to match empirical dynamics by modifying BFolResp. The WUEConst parameter was tuned to produce modeled water use efficiency (WUE) within empirical limits (Limousin *et al.*, 2013). All other parameters (Table 1) were derived from the literature, unpublished data from the experiment or the expert judgment of the authors. When there was considerable uncertainty in a parameter, or when differences in parameter settings resulted in inability to match empirical measures (e.g., wilting point), we tended to use the same or similar values for both species to mitigate the confounding effects of parameter uncertainty on the competitive interactions between the species.

Model testing

We tested the model by simulating the experimental treatments and comparing model output to empirical measurements. Treatments were simulated by modifying the precipitation amounts in the weather stream during the years of the experiment and keeping all other parameters and inputs unchanged. We reduced monthly precipitation amounts by 45% for the drought treatment. The irrigation treatment was typically applied once per month and we added the specific amount of water added (typically 19 mm) to the months when irrigation was applied (Pangle *et al.*, 2012). Similar to model calibration, empirical measures from the treatment plots were compared to the monthly means output by the model.

Quantitative tests of model performance were problematic because most empirical measures were single-day "snapshots" of physiological variables that can vary dramatically within a month depending on the recency of a rainfall event. Soil water was measured every 15 min throughout the experiment, but the model used a constant fraction of monthly rainfall lost to surface runoff and evaporation, which does not account for differences in runoff loss between intense and gentle rain events. Consequently, quantitative comparisons of predictions of monthly mean values to instantaneous (daily) measurements were deemed inappropriate. We therefore relied on visual evaluation of graphical overlays of simulated dynamics and empirical measures, concentrating on the magnitude of predicted values and measurements.

We also sought to assess the ability of the model to predict growth reduction and the likelihood of mortality because of drought stress. Tree cohorts die in the model when the nonstructural carbon (NSC) pool declines to <1% of the combined size of the structural pools (wood and roots) (Sevanto *et al.*, 2013). We expected that the size of the NSC pool would be related to the mortality rate on experimental plots Dickman *et al.*, in press). We plotted the minimum size of simulated NSC pools during the experiment against the proportion of trees that died on each experimental plot.

Future climate scenarios

To heuristically assess the potential utility of the model for projecting tree species response to climate change, we simulated alternative climate change scenarios and assessed the response of the piñon–juniper ecosystem at this site. We evaluated three hypothetical future climate scenarios for the region derived from the literature: (1) warmer temperatures and precipitation similar to the recent past (Gutzler & Robbins, 2011), (2) warmer and drier (Seager *et al.*, 2007), and (3) warmer with delayed onset and withdrawal of the monsoon (Cook & Seager, 2013). Each scenario was generated by modifying the temperature and precipitation values of a historical weather stream, which was used to provide interannual variability. For warmer scenarios, we added 2 °C to each monthly temperature value and for the drier scenario we decreased each precipitation value by 25%. For the delayed monsoon scenario, we pushed the July (monsoon onset) through November precipitation values one month into the future, and moved the December value back to July, keeping annual precipitation unchanged. All future scenarios included modest CO_2 concentration increases from the RCP 3PD peak and decline emissions scenario that peaks at 443 ppm in 2052 (Meinshausen *et al.*, 2011). All other model inputs were unchanged from the calibrated values (Table 1), including the spin-up climate. Each scenario was simulated for 100 years and we plotted response variables of net photosynthesis, woody biomass and size of the NSC pool through time by species.

Results

Model calibration

Calibration using just five tuning parameters produced model behavior consistent (both in magnitude and temporal variation) with the empirical measurements (Fig. 1). Soil water was tuned so that it varied within the range of empirical measurements. Water dynamics generally followed the wet and dry periods seen during the experiment and fell within or near the monthly range of empirical observations. The biggest departure between modeled and empirical measures occurred when the model simulated too much water through the winter, which carried over into the spring when in reality the soil is usually quite dry. In the field, trees are active during winter warm spells, thereby consuming water. However, because the model uses mean monthly temperatures, it is insensitive to these warm spells. Vapor pressure deficit was not a tuned variable, but was calculated by the model from the climate inputs and CO_2 concentration, showing high agreement with empirical estimates. WUE was tuned to vary within the range of empirical measurements, and modeled values exhibited seasonal fluctuations consistent with measured values. Foliar respiration and net photosynthesis were similarly tuned to vary within the range of empirical measurements, and while the model generally followed the temporal variation in empirical measures, discrepancies were related to discrepancies in the

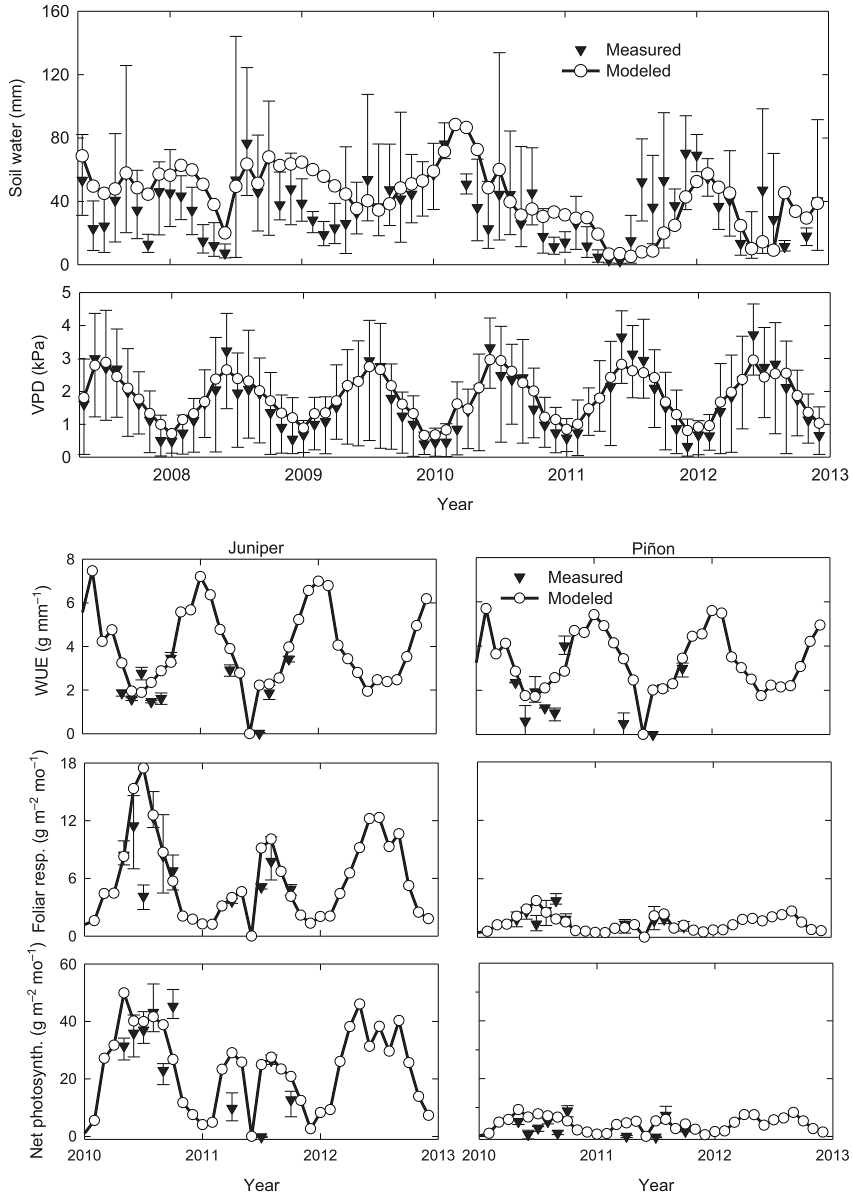

Fig. 1 Calibrated model outputs compared to empirical measurements taken on the ambient control plots. Error bars show the range of empirical measurements.

amount of soil water. That is, when the model overpredicted water it also overpredicted foliar respiration and net photosynthesis. Transpiration showed dynamics very similar to net photosynthesis (not shown). Juniper LAI was empirically estimated in 2006 to range between 0.5 and 0.65 while model predictions ranged between 0.73 and 0.88; piñon LAI ranged from 0.10 to 0.25 and model predictions between 0.32 and 0.39. Some of this discrepancy is related to the fact that there are many gaps in a piñon–juniper canopy while LANDIS-II assumes a continuous canopy.

Model testing

Our tests modified only precipitation inputs and all model outputs were an emergent property of these inputs, model algorithms and calibrated parameters. The model predictions generally followed the seasonal and inter-annual variation in physiological variables, and responded to the treatments in a way similar to that observed in the empirical measurements. Because empirical data were instantaneous measures taken on a single date, they were not completely comparable to model outputs of monthly means. However, they do provide valuable benchmarks to assess model performance. Absolute decreases and increases in photosynthetic activity for both species under drought and irrigation treatments (respectively) generally followed empirical observations of lower productivity under drought and higher under irrigation, but the model tended to dampen the magnitude and rapidity of the empirical fluctuations (Figs 2 and 3). For example, the model underestimated water under the drought treatment, especially during the summer rains (Fig. 2). Overestimation of water in the spring was less of a problem in the drought treatment modeling scenario, because there were lower precipitation inputs and thus less water to carry over through the winter. The model overestimated water under the irrigation treatment, but water did fluctuate in general synchrony with the empirical measures from year to year. Again, the model overestimated water in the winter and spring, but otherwise followed temporal fluctuations.

Both foliar respiration and net photosynthesis tracked the magnitude of variation in empirical measures between wet (2010) and dry (2011) years for both species (Figs 2 and 3), with productivity differences between the species accurately modeled also. The model was less successful at predicting the marked variation within a growing season because of excess modeled water during the dry springs. The model showed that NSC declined under the drought treatment and increased under the irrigation treatment for both species (Figs 2 and 3). The empirical estimates of NSC do not show such clear trends, likely because empirical measures of NSC (% sugar and starch in foliar and woody tissue samples) are difficult to scale to the cohort-level NSC pool tracked by PnET-Succession. However, detailed analysis elsewhere showed that NSC declined under the drought treatment and the irrigation treatment was similar to the control (McDowell *et al.*, 2013; Dickman *et al.*, in press). It is interesting to note that many mature piñon trees under the experimental drought treatment were killed by bark beetles in 2008 and 2009 (Gaylord *et al.*, 2013) and the model predicted that piñon NSC dropped steadily from 4% in 2008 to 1.5% in 2012, with physiological mortality assumed to occur when NSC<1%. Thus, the model predicted that piñon became drought-stressed at the time when many trees succumbed to bark beetle attack. There was a fairly clear relationship between the minimum value of the modeled NSC pool and mortality rate on experimental plots, consistent with observations and with other model analyses (McDowell *et al.*, 2013; Dickman *et al.*, in press), and it appears likely that the NSC pool may serve as a general index of the probability of mortality (Fig. 4).

Future climate scenarios

Water stress increased with reduced precipitation, but the effect of temperature on water stress was minimal (Fig. 5). Increased temperature and decreased precipitation each contributed to a decline in photosynthetic productivity for both juniper and piñon, and productivity generally declined rapidly when cohorts were water-stressed, but recovered less quickly, with piñon never fully recovering from the simulated drought of 2055–2060 (Fig. 5). Consequently, juniper woody biomass declined and recovered, while piñon biomass continued to decline after the drought except under the historical climate scenario (Fig. 6). NSC reserves followed variation in net photosynthesis, with juniper NSC recovering after the drought, while piñon NSC reached a new, lower equilibrium under all scenarios except warmer and drier, where productivity was inadequate to cover respiration costs and the cohort died at year 2076 (Fig. 7b). When water stress was low (prior to 2035), both species maintained about the same level of NSC reserves, but when water became limiting, piñon was less able to maintain reserves. Because NSC levels can serve as an index of mortality risk (Fig. 4), we can predict that piñon would be more vulnerable to mortality than juniper for at least 50 years following the drought ending in 2060 (Fig. 7).

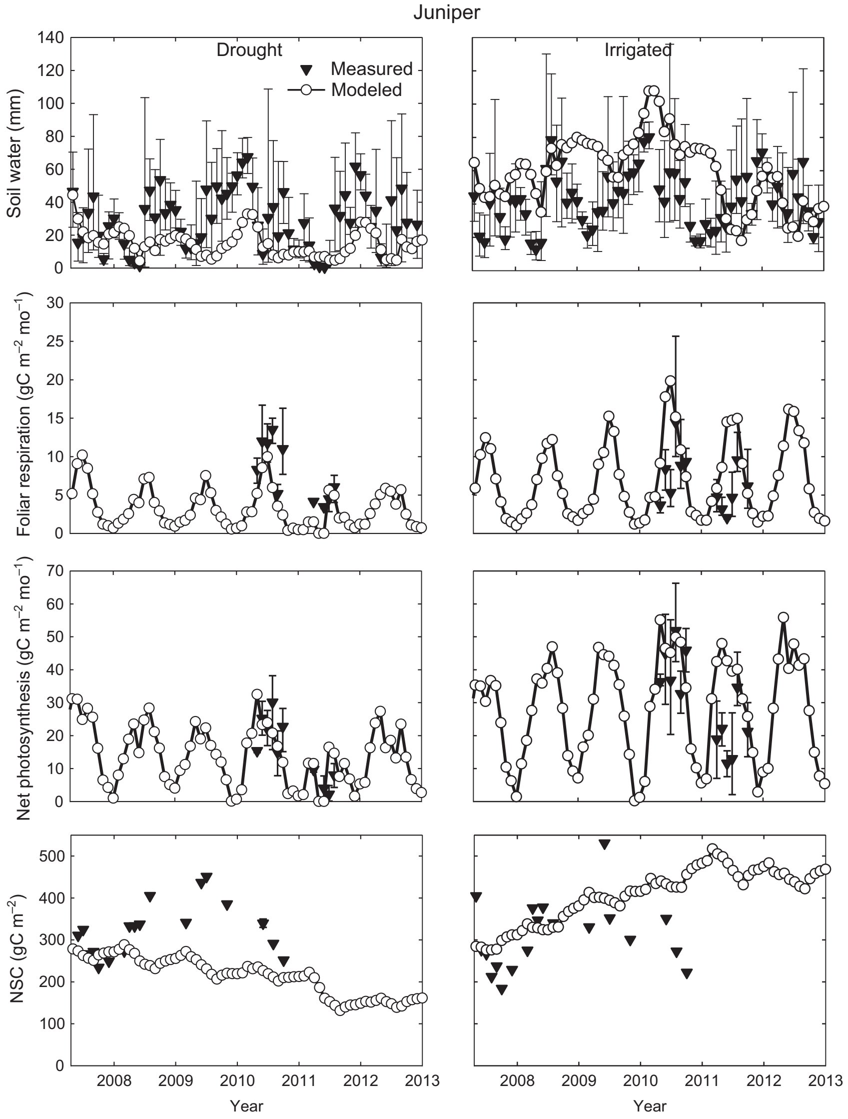

Fig. 2 Model tests comparing simulated and empirical responses of juniper to the experimental treatments. Error bars show the range of empirical measurements.

Discussion

Insights

Our primary objective in this study was to determine if our modeling approach holds promise for projecting drought-induced effects on forest growth and mortality. The pinon-juniper drought experiment provided an ideal data set to address this objective. Although PnET-Succession uses monthly weather inputs and mean site and species physiological parameters and therefore does not simulate some of the intraannual growth dynamics, it nevertheless does a good job of capturing the interannual dynamics of growth and carbon reserves in response to variation in precipitation. For the purposes of landscape modeling of forest growth and succession over long time periods, net photosynthesis is the key output of the model. This variable responded to the treatments similar to the empirical measures. NSC also varied consistently with empirical measures under drought and wet conditions, and shows promise as a surrogate for physiological stress and risk of mortality. These results suggest that this physiologically simple model is well suited to mechanistically simulate drought effects under climate change at broad temporal and spatial scales.

After calibrating the model using only five parameters, model behavior responded appropriately to the treatments as an emergent property. We likely could have generated even closer congruence with

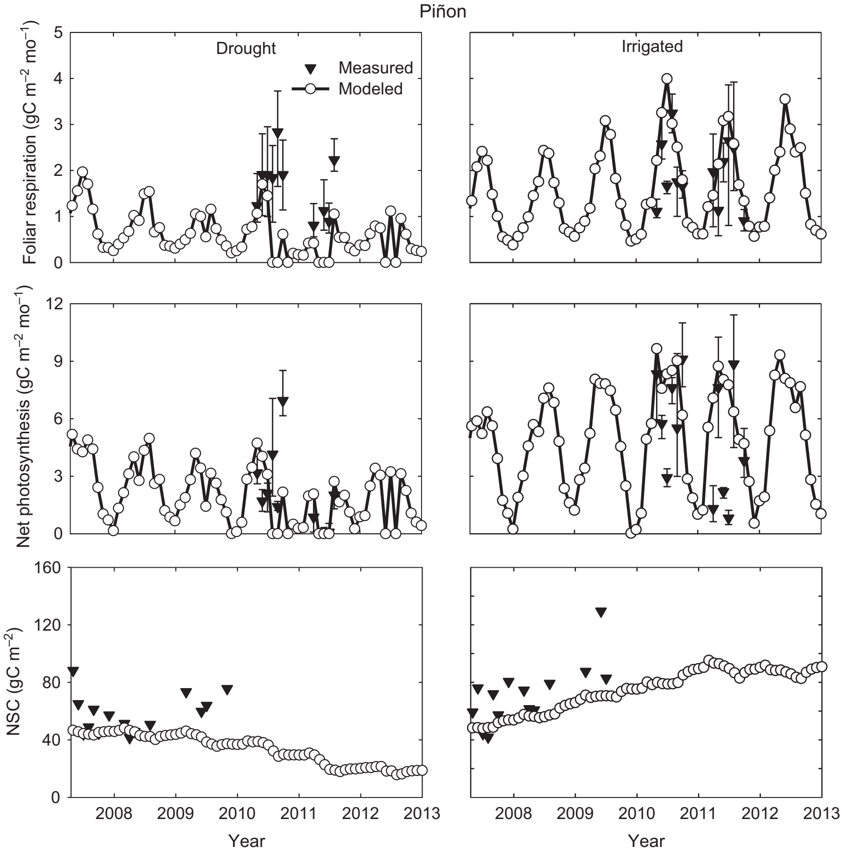

Fig. 3 Model tests comparing simulated and empirical responses of piñon to the experimental treatments. Soil water is identical to Fig. 2. Error bars show the range of empirical measurements.

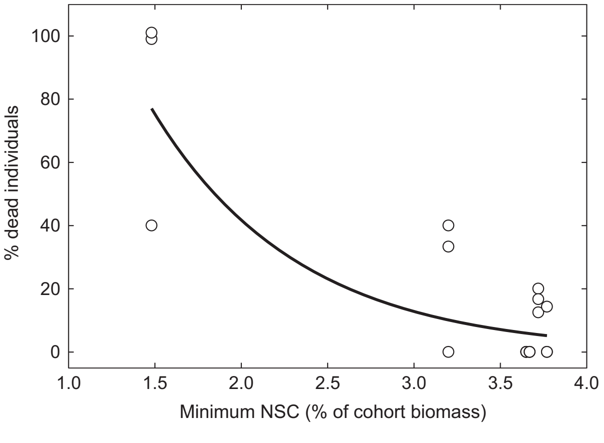

Fig. 4 Relationship between the minimum modeled value of NSC and the empirical observation of the % of individuals on a plot that died. Both species are included and each point represents an experimental replicate of a species-treatment combination.

experimental results if we used plot-specific water holding capacity (WHC) and leaf nitrogen parameters, but our purpose was to test the generality of PnET-Succession for landscape-scale simulations where site-level precision is usually not possible. In the course of our study, we also verified that the model responds in predictable and stable ways to variation in all parameters. That is, there do not appear to be any unintended interactions among parameters that produce erratic and inexplicable fluctuations in output variables when input parameters are varied. This suggests that model structure and its links to the fundamental drivers of precipitation and temperature are sound. However, additional evaluations in other ecosystems are needed to fully confirm the generality of our modeling approach for projecting drought effects on forested landscapes.

Because PnET has performed well in many ecosystems worldwide (e.g., Xu *et al.*, 2009), and because its use within our model performed well in an ecosystem quite different from the ones for which PnET was designed, we expect it to do well in other forest types. Although similar experimental datasets are lacking for most forest types, future studies can determine if PnET-Succession can produce relationships between NSC and length of droughts that are similar to those found by Gustafson & Sturtevant (2013) in the Midwest USA.

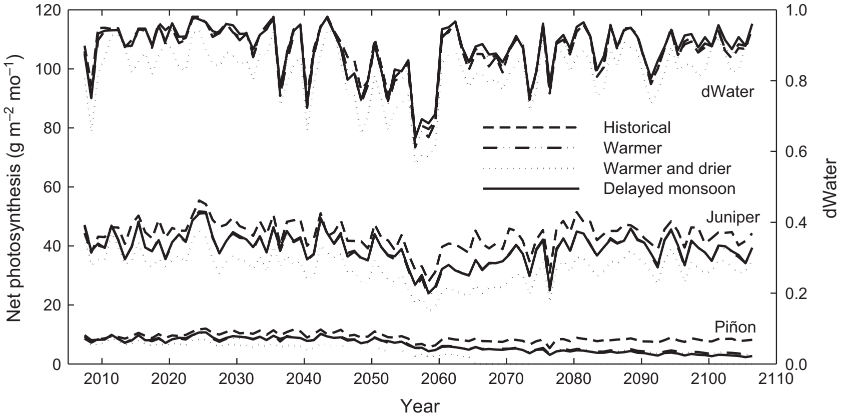

Fig. 5 Simulated photosynthesis under the four future climate scenarios. The PnET-Succession water stress reduction factor (dWater) for piñon is shown for comparative purposes; moisture stress increases as dWater decreases. The Warmer and Delayed Monsoon curves overlap to a great extent.

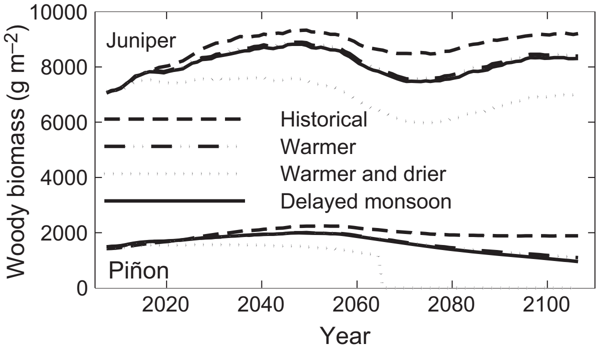

Fig. 6 Woody biomass (roots and stems) under the four future climate scenarios. The Warmer and Delayed Monsoon curves overlap to a great extent.

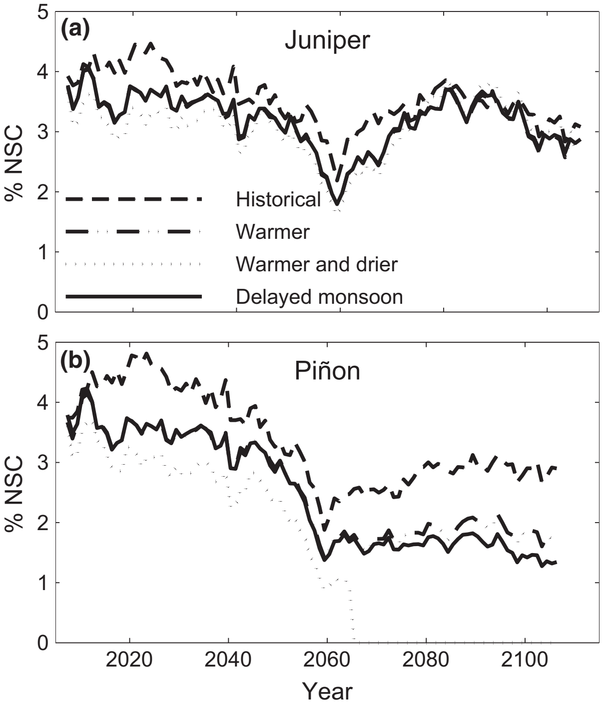

Fig. 7 Relative size of the NSC pool (carbon reserves) under the four future climate scenarios. The Warmer and Delayed Monsoon curves overlap to a great extent.

Most ecosystem process models lack any representation of mortality (McDowell *et al.*, 2013). Many FLMs already include disturbance by agents that are more likely to kill stressed trees than nonstressed trees (e.g., insects). However, few actually link the simulation of such disturbance to a measure of tree stress, and when they do, the measure of stress is typically a surrogate for physiological stress. For example, a modification to the Biological Disturbance Agent extension of LANDIS-II (Sturtevant *et al.*, 2004) allows use of climate variables such as the Palmer Drought Severity index as a surrogate for tree stress. Temperli *et al.* (2013) linked disturbance by European spruce bark beetle (*Ips typographus*) to multi-scaled drivers including an index of spruce drought stress. Given the linkage between drought stress and bark beetle disturbance across multiple ecosystems (Raffa *et al.*, 2008; Gaylord *et al.*, 2013; Williams *et al.*, 2013) there is potential to link NSC levels simulated by PnET-Succession to attack by agents such as bark beetles, thereby more mechanistically simulating the interaction of drought stress and mortality by other proximate causes.

The success of our model at predicting tree species' response to drought suggests that it should also improve a number of issues currently plaguing FLMs: (1) growth and competition can better respond to weather extremes than approaches that use only annual or decadal climate means, (2) physiological stress (as indexed by the relative size of the NSC pool) is used directly to cause mortality (when NSC <1%), and can be passed to disturbance extensions to influence susceptibility to specific disturbance intensity (e.g., if stressed trees are more susceptible to mortality by a ground fire than nonstressed trees, then simulation of fire effects could be improved with information about physiological stress of cohorts), and (3) PnET-Succession provides a robust way to scale site-level physiological relationships to landscape scales. The ability of most site and stand-level physiological models to make predictions about the future of specific sites is limited by their inability to account for disturbances and other spatial processes such as dispersal. The ability of most FLMs to simulate forest growth and succession as a function of the fundamental drivers of water and temperature is limited because of a reliance on phenomenological relationships that were estimated under conditions of the past. Such an approach was adopted primarily because more mechanistic approaches have much greater levels of complexity, and therefore, uncertainty. However, it is becoming increasingly clear that a phenomenological approach requires too many *ad hoc* assumptions when making projections for the novel environmental conditions of the future (e.g., successional transition probabilities, future growth rates under interacting temperature, precipitation, and CO_2 trends), and the uncertainty introduced by such assumptions is greater than that of more mechanistic approaches (Gustafson, 2013). However, in PnET-Succession, the links to the fundamental drivers of climate are very strong, and the first principles approach is expected to be quite robust to novel environmental conditions of not only climate, but also increased levels of pollutants such as CO_2 and ozone (Ollinger *et al.*, 2002). PnET-Succession attempts to strike an appropriate balance between complexity and simplification that is appropriate for landscape spatial and temporal scales. Our results suggest that the model provides a good response to the fundamental drivers of water and temperature. Additional study is required to evaluate the generality of the approach to other drivers (e.g., CO_2 and ozone) and in other ecosystems.

The scenario simulations illustrated the ability of PnET-Succession to integrate the interacting effects of species vital attributes and novel temperature, precipitation, and CO_2 regimes to produce quantitative projections of species growth, competition, and carbon reserves that allow insightful comparisons of scenarios. All future scenarios had lower productivity, biomass and carbon reserves than the historical scenario, with the warmer and drier scenario suffering the greatest losses. The delayed monsoon scenario was mostly indistinguishable from the warmer scenario, although NSC reserves did tend lower for piñon under the delayed monsoon scenario, suggesting that a delay of the monsoon rains may increase the mortality risk of piñon, which is less able to withstand prolonged drought events. Our results also suggest that piñon may be unable to persist at this site if the climate becomes warmer and considerably drier, likely because it will be less able to rebuild sufficient carbon reserves after severe drought events, consistent with Williams *et al.* (2013).

Major assumptions

Our study made some important assumptions. (1) We assumed that approximate soil parameters are sufficient to model the water budget across a range of sites. In LANDIS-II, soil parameters are specified by ecoregions, which are defined as landscape-scale spatial zones where growing conditions and disturbance regimes are relatively homogeneous. The experimental plots we simulated had some variation in soil WHC, but the variation was likely less than is typically seen within a LANDIS-II ecoregion. (2) LANDIS -II assumes that cohorts are spatially homogeneous within a site (grid cell), which in our study was 1600 m^2. This is the first test of PnET-Succession in an ecosystem that does not typically exhibit complete canopy closure. Although the model consequently overestimated LAI for the site, model projections of most other variables matched empirical measures because they were expressed on a m^2 basis. (3) We assumed that a carbon starvation mechanism is a reasonable surrogate for all mortality mechanisms (e.g., hydraulic failure and biotic agent mechanisms; McDowell *et al.*, 2011), producing a similar outcome for most drought events. This assumption is untested and there is considerable uncertainty about the specific mechanism of death by hydraulic failure in the literature, but there is some support for our assumption (Hartmann *et al.*, 2013; McDowell *et al.*, 2013; Quirk *et al.*, 2013; Sevanto *et al.*, 2013; but see Sala *et al.*, 2010).

Caveats

Water drives this system and the model has a coarse representation of hydrology dynamics. Our approach was designed to respond to droughts that persist for many months or years, and our results suggest that the model did well at simulating drought events at that scale. It did less well at simulating water dynamics that are driven by daily conditions, such as winter warm spells and individual rain events. Semiarid woodlands in the Southwest US can experience significant temperature swings in winter (Pangle *et al.*, 2012) and these dramatic temperature swings can routinely result in daytime environmental conditions that are favorable for substantial evapotranspiration, even when minimum temperatures fall below 0 °C. Because the model uses monthly mean temperature to drive photosynthesis, it was unable to simulate this winter and early spring transpiration that occurs at our site, therefore overestimating winter and spring soil water in many years. The use of monthly mean precipitation also affected modeled soil water dynamics during the summer when soil water usually limits photosynthesis. Typically, the premonsoon period (April–June) at this site is dry and soil water is quite limiting. The monsoon period (July–September) produces rain events that are of short duration and high intensity (Plaut *et al.*, 2013), and both piñon and juniper respond to pulses of precipitation that are quickly transpired and/or evaporated from the system on the order of days to weeks (Plaut *et al.*, 2013). The use of mean monthly precipitation in the model does not allow response to frequent and small pulses of precipitation. Furthermore, the model does not account for variation in surface runoff that is proportional to the intensity of rainfall events. This created a situation where modeled photosynthesis lagged empirical observations, and only recovered once substantial inputs of precipitation had been received. Another factor contributing to water discrepancies may be that we did not model transpiration by shrubs and herbaceous plants, but these are a minor component of the ecosystem and we included this loss of water in the PrecLossFrac parameter. Despite our simplifications, the model did quite well at capturing the annual and interannual variations in precipitation and simulated soil water availability.

For variables such as net photosynthesis, foliar respiration, and WUE, the differences between modeled and measured physiological variables (net photosynthesis, foliar respiration, and WUE) were largely the result of differences in the temporal scale of model inputs and outputs (monthly averages) and the empirical measures (instantaneous/daily). The model outputs tended to overestimate physiological measurements, but there was no systematic bias. Differences between simulations and measurements were usually explained by the timing of the measurements, with empirical measures taken after a dry period within an otherwise wet month (e.g., July 2010) being less than model predictions, and measurements taken after a moisture pulse in a dry month (e.g., October 2010) being higher than predictions. Other differences were explained by the tendency of the model to overpredict water availability (and therefore physiological variables) during spring (e.g., April 2011). Short-term (days to months) variations in water availability and physiological variables are particularly large in this semiarid system where precipitation is strongly seasonal and tree physiology is driven by relatively short periods of soil moisture availability following rainfall events (Williams & Ehleringer, 2000; Plaut *et al.*, 2013). The temporal resolution of our modeling approach was unable to precisely simulate such short-term variations, but it is likely that the model would perform better in environments with a less variable water supply. The model was better able to simulate temporal variations in net photosynthesis for juniper, which has a better ability to extract deep soil water and relies less on short-term moisture pulses than piñon (Williams & Ehleringer, 2000; West *et al.*, 2007), which is strongly pulse-driven and performs photosynthesis only during short windows of available soil moisture because of its isohydric behavior (Plaut *et al.*, 2012; Limousin *et al.*, 2013).

McDowell *et al.* (2008) argue that some tree species do not close their stomata when water-stressed and are killed when air bubbles enter the xylem and prevent water transport (hydraulic failure). PnET-Succession does not model hydraulic failure because it is particularly difficult to model, especially at this scale (McDowell *et al.*, 2013). Evidence from this site suggests that while the process of hydraulic failure may occur, carbon starvation appears to dominate the mortality of both piñon and juniper (McDowell *et al.*, 2013). This process is not well understood and would be difficult to model at the scale at which LANDIS-II operates. We have assumed that a carbon starvation mechanism is a reasonable surrogate for the hydraulic failure mechanism, but our model may underestimate growth reduction for species that close their stomata when water-stressed to prevent hydraulic failure and underestimate mortality for species that do not, especially when drought is short, but intense. However, there is considerable evidence that the length of drought is more likely to result in tree mortality than the intensity of drought (Guarin & Taylor, 2005; McDowell *et al.*, 2008; Gustafson & Sturtevant, 2013). In future work, we will explore if the GrMstSens parameter can be used to better mimic the response to drought of species prone to hydraulic failure.

Future work

Our study opens a door to a wide range of promising opportunities that should be explored. Piñon and juniper are both very drought tolerant, which sets a high bar for modeling and detecting drought effects. Our success here does not preclude the need to evaluate the ability of PnET-Succession to model drought effects for other species. Our model test was conducted at the dry end of the range of the piñon–juniper ecosystem. It would be instructive to apply the model to other parts of the range that are less arid. We did not formally test the ability of the model to predict the effects of temperature changes on physiological variables, but our simulation of alternative climate scenarios suggests that there is a reasonable relationship between climate (both temperature and precipitation) and species response. Neither did we test the ability of the model to predict the effects of elevated CO_2 concentrations on growth and drought resistance, but the PnET functions in the model will allow this to be done in future studies. Also, our study did not use the spatial capabilities of LANDIS-II. Because piñon–juniper ecosystems can be structured by fire, insect outbreaks and barriers to seed dispersal, important insights could be gained by exploring the spatial (landscape) consequences of climate change on this system. Most importantly, the possibility must be explored that our model will adequately simulate drought and temperature effects in less arid and more complex forest ecosystems, where a wider range of drought tolerance exists among species.

We draw three main conclusions from our study. (1) With only modest calibration, PnET-Succession predicted physiological response of piñon and juniper to drought and irrigation treatments with remarkable effectiveness. (2) PnET-Succession produced quantitative projections of piñon–juniper physiological response to future climate scenarios. The relative size of NSC reserves can be used to estimate the relative risk of mortality of each species through time under various scenarios, which could be a very useful metric for climate change studies. (3) The stronger links between fundamental drivers and growth rates in PnET-Succession hold great promise to improve the rigor of LANDSI-II for scaling the effects of climate change to the landscape scale, and this approach is expected to be more robust to the novel environmental conditions of the future because of its greater reliance on first principles.

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