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Climate and Bark Beetle Effects on Forest Productivity — Linking Dendroecology with Forest Landscape Modeling

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Climate and bark beetle effects on forest productivity: linking dendroecology with forest landscape modeling

Climate and bark beetle effects on forest productivity: linking dendroecology with

forest landscape modeling

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Running head: Stand to landscape level ANPP

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LANDIS-II;

Abstract

water deficit, CWD) and bark beetles on basin-wide ANPP from 1987-2006, estimated through

10 tree core increments and a landscape simulation model (LANDIS-II). Tree ring data revealed the

14 ANPP increased throughout thi In forested systems throughout the world, climate influences tree growth and aboveground net primary productivity (ANPP). The effects of extreme climate events (i.e. drought) on ANPP can be compounded by biotic factors (e.g. insect outbreaks). Understanding the contribution of each of these influences on growth requires information at multiple spatial scales and is essential for understanding regional forest response to changing climate. The mixed conifer forests of the Lake Tahoe Basin, California and Nevada, provide an opportunity to analyze biotic and abiotic influences on ANPP. Our objective was to evaluate the influence of moisture stress (climatic tree core increments and a landscape simulation model (LANDIS-II). Tree ring data revealed that ANPP increased throughout this period and had a nonlinear relationship to water demand. Simulation model results showed that despite increased complexity, simulations that include moderate moisture sensitivity and bark beetle outbreaks most closely approximated the field-derived ANPP ~ CWD relationship. Although bark beetle outbreaks and episodic drought-induced mortality events are often correlated, decoupling them within a simulation model offers insight into assessing model performance as well as examining how each contributes to total declines in productivity.

Introduction

Forests are an integral component of the global carbon (C) cycle, sequestering approximately 30% of annual anthropogenic C emissions (Pan et al. 2011 a). Estimates of forest C dynamics are dependent on reliable forest growth and productivity patterns as influenced by climate and disturbances. Forecasts of forest response to changing future climatic conditions require quantification of the relative importance of key influences on tree growth, mortality, and regeneration, which can vary regionally (Chen et al. 2010; Laura Suarez and Kitzberger 2010; Fisichelli et al. 2012). Regional and local disturbances such as wildfire, drought, or insect outbreaks, which are all influenced by climate variability, will interact to affect future forest dynamics in novel ways. Simulating these interactions is critical for understanding future forest trajectories (Kurz et al. 2008; Adams et al. 2009; Bentz et al. 2010).

se interactions is considered.
 al. 2009; Bentz et a
 Draft is denoted in the growth is denoted. Quantifying the response of forest productivity to climate variability and disturbances requires information at multiple scales. Individual tree growth is determined by inter- and intra-annual climate patterns, topographical and edaphic factors, age-related growth patterns, biotic interactions, and disturbances (Fritts and Swetnam 1989). Measures of annual growth increment at the individual tree scale are useful for determining site-specific factors affecting growth. While abiotic (climatic and edaphic) factors and endogenous biotic factors (e.g. ungulate browse) may be the primary determinants of growth during early succession (before canopy closure), in more closed canopy conditions, density-related competition may supersede abiotic influences on growth (Hurteau et al. 2007, Kuijper et al. 2010). At the landscape-wide scale, measures of growth help reveal the influence of regional climate patterns such as the Pacific North American pattern, rather than finer scale biotic determinants of productivity such as individual tree competition (Trouet and Taylor 2009).

Individual tree growth is also affected by disturbances in non-uniform ways as a result of physiological responses to stress, damage, or altered stand characteristics. Insects, such as bark beetles, alter tree growth patterns through increased mortality of older, larger trees, creating canopy gaps and releasing younger cohorts and understory vegetation (Klutsch et al. 2009). Species-specific differences in response to moisture stress can also result in substantial variability in forest growth and carbon (Earles et al. 2014; Hurteau et al. 2007). Moisture stress and bark beetles have also been shown to interact in nonlinear patterns, capable of enhancing or detracting from the effects of the other depending on forest condition and topographic setting (Temperli et al 2013). The combination of disturbance effects and individual tree species physiological response to changes in climate, particularly severe drought, creates complex overall forest growth patterns.

Canceles Curve
ductivity in a future While empirically-derived relationships (e.g. site index curves) have been used for decades to predict tree growth, modeling forest productivity in a future climate requires capturing the underlying processes that govern regeneration, growth, and mortality (Bontemps and Bouriaud 2013; Gustafson 2013). Models of forest growth must integrate the most influential factors at the scale appropriate for the questions being asked. For instance, site productivity models of even-aged stands may need only basic soils and climate information to approximate observed patterns (Skovsgaard and Vanclay 2008). Ecosystem or landscape models rely on coarse-scale growth responses to temperature and precipitation fluctuations, as well as effects from disturbances (Law et al. 2004; Pan et al. 2011 b; Scheller et al. 2011; Loudermilk et al. 2013). Coupling fine-scale (individual tree) empirical estimates and landscape-scale model projections of productivity provides an opportunity to compare growth estimations across multiple scales.

The objective of this study was to quantify the influence of moisture availability, as measured by climatic water deficit (CWD), on forest productivity using tree core data and to compare those scaled *in situ* estimates of ANPP with outputs from a landscape simulation model (LANDIS-II) to evaluate two factors, moisture sensitivity and bark beetle outbreaks, that influence ANPP in the model. We examined the individual and additive effects from these two factors as simulated by our model and compared simulated ANPP to field-derived estimates of ANPP over a 20 year period. Additionally, we analyzed the merits of each ANPP estimation approach and discuss these in relation to the drivers of forest growth.

Materials and Methods

Study area

of low elevation fo
a and Nevada, USA
recipitation primat 76 Our study area consisted of \sim 31,000 ha of low elevation forested land within the Lake Tahoe 77 Basin (LTB), on the border of California and Nevada, USA (Figure 1). The climate is Mediterranean, with dry summers and precipitation, primarily winter snow, occurring mostly from October-May. Temperature and precipitation are largely controlled by the basin-like topography, which ranges in elevation from 1897 (lake level) to 3320 m; seasonal high and low temperatures decrease with increasing elevation. Soils are primarily of shallow granitic substrate with ancient volcanic bedrock lining the north shore (Rogers 1974). Primary tree species include Jeffrey pine (*Pinus jeffreyi*), sugar pine (*P. lambertiana*), white and red fir (*Abies concolor, A. magnifica*) and to a lesser extent incense-cedar (*Calocedrus decurrens*), whitebark pine (*P. albicaulis*), western white pine (*P. monticola*), and lodgepole pine (*P. contorta*) (Graf 1999). Within the basin there are several distinct forest types including mixed conifer-white fir stands 87 (lake level to \sim 2100m elevation), Jeffrey pine dominated stands (lake level to \sim 2400m), mixed

88 red fir-western white pine stands $(\sim 2100$ to ~ 2600 m), lodgepole pine-dominated stands $(\sim 2400 + -100)$ 3320 m) , and subalpine stands of whitebark pine or mountain hemlock (*Tsuga mertensiana*) (~2600-3320 m). Old-growth stands and stands dominated by sugar pine exist within the LTB, 91 but are rare. Extensive logging during the $19th$ century, followed by aggressive fire suppression activities have shifted forest structure towards dense, young forests (<120 years old) (Beaty and Taylor 2008).

94 *Tree ring estimates of ANPP*

attributes were
propertify (DBH) we
1/10th ha subplot, a
1 the same plot cent 95 We used field data collected at two to four plots in each of 21 creek drainages (52 total plots) 96 ranging from 1900-2200 m elevation during summer 2009 to develop our empirical ANPP 97 estimate (Figure 1) $_{Table S1}$. Forest structural attributes were measured using a nested design in 98 which all trees \geq 80 cm diameter-at-breast height (DBH) were measured in a 1/5th ha plot, all trees > 50 cm DBH were measured in a $1/10^{th}$ ha subplot, and all trees > 5 cm DBH were 100 measured in a $1/50th$ ha subplot, all with the same plot center. Within each plot two to three 101 individual live trees were selected for coring from the five smallest and five largest individuals 102 (Hurteau et al. 2014). Visual cross-dating of tree cores was conducted using characteristic rings 103 and checked with COFECHA (Stokes and Smiley 1968, Holmes 1983). Summary statistics were 104 calculated using the dplR package in R and are presented in supplemental material $_{\text{Table S2}}$ (R 105 Core Team 2015, Bunn et al. 2015). The cored tree sample size by species approximated the 106 proportional contribution of each species to mean basal area after excluding cores that could not 107 be cross-dated $_{\text{Table S3}}$.

108 Annual ring widths were measured to the nearest 0.001 mm using Windendro (Regent

109 Instruments, Inc) and error prone cores were re-measured using a Unislide TA measuring system

We selected the period from 1987-2006 because it had the highest number of available tree core samples and high resolution data of a large basin-wide bark beetle outbreak that began in 1988 (discussed below). Over the study period, maximum summer temperature ranged from 14 to 130 18.5°C, and minimum January temperature ranged from -4.2 to 0.8°C, according to the 4km

Landscape projections of ANPP

We used the landscape disturbance and succession model, LANDIS-II, to model ANPP across the LTB (Figure 3) (Mladenoff et al. 1996; Scheller et al. 2007). The LANDIS-II model was previously parameterized for the LTB to simulate landscape carbon dynamics under contemporary and future changing climate (Loudermilk et al. 2013, 2014). LANDIS-II is a spatially explicit, raster-based process model and represents trees in species-age cohorts. The model incorporates tree species life history attributes (e.g. longevity, shade tolerance, drought tolerance, seed dispersal distance, etc.) that allow each species to respond uniquely to light, nutrient, and water availability, local climate, soil conditions, and disturbance. LANDIS-II has

- been applied in many forested ecosystems (Swanson 2009; Cantarello et al. 2011, Gustafson and
- Sturtevant 2012), and calibrated using a variety of available resources, including eddy flux
- towers (Scheller et al. 2011) and FIA-derived biomass estimates (Thompson et al. 2011). ANPP
- calibration in the LTB (Loudermilk et al. 2013) was based on literature values of ponderosa pine
- plantations in the Sierra Nevada (Campbell et al. 2009).

Century Succession extension

Carbon dynamics were modeled using the Century Succession extension ('*Century*') for

LANDIS-II, which is based on the CENTURY soil model (Parton et al. 1983). *Century* was

calibrated and validated with available data to satisfy five model output targets: aboveground net

162 primary productivity (ANPP), Net Ecosystem Production (NEP), aboveground live biomass, soil

163 organic C (SOC), and soil inorganic nitrogen (mineral N) (Loudermilk et al. 2013). Further

164 details on model developm

organic C (SOC), and soil inorganic nitrogen (mineral N) (Loudermilk et al. 2013). Further

details on model development, parameterization, and calibration are in Loudermilk et al. (2013)

and Supplemental Materials.

Century utilizes monthly climate data, which influences tree establishment, growth, and

regeneration (Scheller et al. 2011). Individual species' growth response to available soil moisture

is dictated by two parameters; these parameters are assigned to broader functional groups to

which each species belongs and dictate moisture sensitivity by determining the ratio of available

water content (AWC) to potential evapotranspiration (PET). The first parameter

('DroughtIntercept', in *Century*: 'pprpts2') determines the effect of AWC on the intercept of this

- relationship, therefore if this value is increased, the intercept is raised and higher AWC is
- required to achieve the same PET. The second parameter ('DroughtRatio', in *Century*:
- 'pprpts3') is the minimum ratio of AWC/PET at which there is no restriction on production,

175 effectively determining the minimum AWC necessary for any growth to occur. The LANDIS-II

Kretchun et al. Stand to landscape level ANPP

congruent with field site disturbance history over the study period.

Page 11 of 98

Kretchun et al. Stand to landscape level ANPP

Biological disturbance agent (BDA) extension

Bark beetle outbreaks were simulated using the Biological Disturbance Agent (BDA) extension for LANDIS-II (Sturtevant et al. 2004). This extension simulates tree mortality that results from outbreaks of insects and disease. We parameterized host species preferences for three bark beetle species active in the LTB, and deterministically set the length and initiation year of a simulated outbreak using a documented outbreak in the LTB that began in 1988. BDA does not utilize climate data to influence beetle activity; within this study it is used as a species-specific stochastic mortality agent parameterized and calibrated to match observed patterns of historical beetle disturbance. The details of this extension and its parameterization are discussed briefly below and in detail in the Supplemental Material.

Individual.
 Draft
 Draft Three bark beetle species were modeled: the Jeffrey Pine Beetle ('JPB'), the Mountain Pine

Beetle (*Dendroctonus ponderosae,* 'MPB'), and the Fir Engraver Beetle (*Scolytus ventralis,*

'FEB'). Although there are other beetles active in the area (e.g. Red turpentine beetle,

(*Dendrocotonus valens*)), these three beetles are responsible for the majority of the recorded

damage in the LTB and there is very little overlap in host species. Empirical data from the

literature and expert opinion were used to determine host species and ages most preferred by

213 each of the three modeled beetle species $_{Table S7}$. JPB and FEB are limited in their primary host

selection (Jeffrey pine and red/white fir respectively), whereas MPB is more of a generalist,

impacting a variety of pine species across the basin (Cole and Amman 1980; Ferrell 1994;

Bradley and Tueller 2001; Walker et al. 2007; Egan et al. 2010). Beetle dispersal is modeled

217 within BDA, defined at an annual rate $(m \text{ year}^{-1})$.

Tree Ring and Model Estimate Comparison

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ts was determined l
WD values. ANOV
dentified by the piec
as the response, wh We calculated median ANPP values and 95% confidence intervals from empirical data using bootstrapping with 500 draws from all field sites (tree ring-derived ANPP estimates) and by using all grid cells from each scenario (31,291 grid cell landscape) for median values and confidence intervals from the simulation outputs. All replicate outputs for a particular modeling scenario were combined, such that all statistical analyses were applied to a 'sample' consisting of all five replicates simultaneously. Median ANPP values were also used to construct statistical relationships for each ANPP estimation method and the BCM-estimated annual average CWD. Regressions were constructed using a linearization technique for estimating regression lines with one or more unknown break points (Muggeo 2003). Upper and lower limits of these piece-wise regressions were set at the minimum and maximum CWD values (23.6, 52.7 respectively) for the study period. The number of break points was determined by the number of integers (29) between the minimum and maximum CWD values. ANOVA was used to compare ANPP above and below the CWD breakpoint value identified by the piece-wise regression within each model scenario. In the ANOVA test, ANPP was the response, while CWD was used as the predictor with an interaction term designating above or below the CWD threshold. Two ANCOVA tests 255 were used to compare the slopes of $ANPP \sim CWD$ relationships between scenarios. In the ANCOVA tests, the five scenarios were evaluated by statistically comparing the slope of the ANPP~CWD relationship between each scenario above the CWD threshold (test 1) and below the CWD threshold (test 2). All statistical and graphical analyses were done using the R statistical software platform (R Core Team 2015, Bivand et al. 2015, Hijmans 2015, Wickham | 2009).

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Results

relationship with increasing CWD until 41mm and a strong negative relationship with increasing CWD above 41mm (Figure 5), as determined through a piece-wise regression technique. This

response was consistent for both empirical and simulated ANPP under all four modeling

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scenarios. ANOVA results demonstrate this differential response in ANPP above and below this CWD cutoff point is significant (F = 5.27, p = 0.024).

- The LowM-noBB scenario consistently had the highest median ANPP values, while the HiM-BB
- had the lowest (Figure 5). The regression slopes of the two scenarios that did not include bark
- beetles had a stronger negative response to higher CWD values (slopes: LowM-noBB= -11.1,
- HiM-noBB= -9.9) than those scenarios that included bark beetles (slopes: LowM-BB= -7.3,
- HiM-BB= -6.8) as well as the tree ring scenario. ANCOVA results reveal that model scenarios
- ANPP ~CWD relationships are statistically different from one another, both below the CWD
- 292 cutoff (F = 10.6, p << 0.005) and above it (F = 17.6, p < 0.005) $_{\text{Table S8}}$.

Discussion

Draft
 Draft Forest productivity is influenced by a number of biotic and abiotic factors in conifer forests of the Sierra Nevada, such as available soil moisture (Dolanc et al. 2013), natural disturbances (bark beetle outbreaks, wildfire), as well as land-use legacies (past clear-cutting), and management (forest thinning for fuels reduction). By comparing our simulated ANPP results to empirical ANPP estimates from tree-core data during a time period with multiple interacting disturbances, we were able to quantify how bark beetles and moisture sensitivity influenced the relationship of ANPP to moisture deficit (CWD).

CWD thresholds for mortality via cavitation have been demonstrated in certain species in

- western mixed conifer forests, and predictive models of species mortality built on these
- thresholds perform well at landscape scales (Anderegg et al. 2015). Similarly, our tree ring-
- derived ANPP estimates indicate a similar inflection point when CWD~41, beyond which
- moisture stress causes a rapid decrease in site-scale growth rate across this landscape (Figure 5).

Year to year, the two scenarios that most closely approximated the field-based ANPP data were the 'LowM-BB' and 'HiM-noBB' scenarios (Figure 4). However, when looking at growth rate as a function of moisture stress, the 'LowM-BB' scenario had a more similar response to empirical ANPP with increasing CWD than the 'HiM-noBB' scenario (Figure 5). Further, the regression slopes of the two scenarios that excluded bark beetles (LowM-noBB= -11.1, HiM-noBB= -9.9) were more negative with increasing CWD than the scenarios that included beetles (LowM-BB= - 7.3, HiM-BB= -6.1) and the slope for the empirical relationship (-7.5). ANPP differences

Page 17 of 98

Canadian Journal of Forest Research

Kretchun et al. Stand to landscape level ANPP

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uestration (Stinson Lower parameterized moisture sensitivity, coupled with the simulation of bark beetles ('LowM-BB scenario') provides a more mechanistic representation of the coupled processes affecting forest productivity during this timeframe because of the clear biological link of drought and beetle attack (Guarín and Taylor 2005; Hebertson and Jenkins 2008; Creeden et al. 2013) and the prevalence of bark beetles in the LTB (Bradley and Tueller 2001; Walker et al. 2007; Egan et al. 2010). Excluding bark beetles, given their known occurrence, fails to capture the biological feedbacks in the system, and ignores a critical disturbance agent that causes forest mortality with subsequent long-term effects on succession and species composition. This is supported by other inventory-based studies, which demonstrate that mountain pine beetle in particular is an episodic control on forest growth and carbon sequestration (Stinson et al. 2011). And although the 'HiM-noBB' scenario may be a more parsimonious model than the 'LowM-BB scenario', it may be misleading to represent this landscape as both a highly moisture sensitive system not influenced by bark beetle outbreaks rather than the opposite, despite the increased model complexity. Furthermore, where drought-induced bark beetle outbreaks are common, the inclusion of both factors is important for long-term simulations of realistic climate-forest dynamics. For instance, the 'pulse' type disturbance of bark beetle outbreaks and insect-host specificity can create landscape patterns of mortality, recovery, and ANPP different from those from a 'press' type disturbance, such as climate-induced moisture stress (e.g. Simard et al 2012).

Finally, our use of tree-ring estimates of ANPP provide a novel and critical validation for projections of ANPP, particularly where eddy covariance flux towers (e.g., Scheller et al. 2011)

are lacking or inventory sampling is too infrequent to capture important year-to-year variation. Such data assimilation approaches provide the opportunity to improve models and their forecasts by leveraging information on past and current states of an ecosystem (Luo et al. 2011), and are becoming increasingly critical as expectations for model projections of management outcomes increase (Clark et al. 2001).

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way account for the the
properties of the standing
mate. Our results should be considered in the context of the limitations of both the empirical and simulation approaches. Our empirical ANPP estimates are potentially limited because they do not account for trees that died within plots prior to the sampling period. Live tree mean basal area was 44.2 (se = 12.8) m² ha⁻¹ and standing dead tree mean basal area was 8.8 (s.e. = 7.9) m² 361 ha⁻¹. Our empirical ANPP estimates do not include productivity from trees that were alive for only part of the 20 year period because many of the standing dead trees were not physically sound and able to be extracted. This may account for the three years in which the 'LowM-BB' and 'HiM-noBB' were higher than the empirical estimate.

Although we explored two processes that influence ANPP at multiple scales, many critical processes were excluded by design or necessity in the simulation model. Wildfires and forest thinning were not included in our simulations because there was no evidence of recent fire or thinning practices within the stands selected for tree coring. Though dispersal and host preferences are included, insect physiology is not directly modeled within the BDA extension. Therefore climate influence on insect population development and dynamics are absent from this study. In our study, we sought to match the temporal and overall spatial patterns of an observed outbreak, therefore, the known drought trigger of beetle outbreaks was incorporated. By deterministically setting outbreak duration, our simulations do not include beetle climate sensitivities, which could have revealed significant changes to reproductive success during

Page 19 of 98

Canadian Journal of Forest Research

Kretchun et al. Stand to landscape level ANPP

warmer periods similar to Jonsson et al (2012). Stochastic behavior was expressed through site selection of beetle mortality, which is influenced by food resources on and around that site. Previous research has shown mortality rates differ amongst tree size and age classes, effects which are further augmented by stand density (Egan et al 2016). Our simulations account for these differences, by determining different susceptibility rates of species-age classes. However, factors that determine an individual tree's likelihood of being killed (e.g., infestation by red turpentine beetle, placement in a particularly dense stand, microsite enhancement of drought stress) are not explicitly represented within our model, which operates on species-age cohorts. Were these factors taken into consideration, we likely would have seen higher variability of within-stand mortality emerge, as individual trees would have been affected rather than entire cohorts.

Management Relevance

Our results are particularly relevant to basin-wide management given the additive effects of disturbance and climate on white fir-dominated areas – the primary target species for extensive fuel treatments (Syphard et al. 2011). In many of the stands with the highest potential ANPP, white fir comprises greater than 50% of the basal area. This highly productive and prolific seeder is more sensitive to drought conditions compared to other species in the region, though fir reproduction in the region continues to be substantial (Hurteau et al. 2007; Earles et al. 2014). Fir-dominated stands in general show a rapid growth potential, yet sensitivity to moisture limitation and insects add a layer of complexity to the existing goals of fuels reduction and carbon sequestration. Management decision making is further complicated by the more frequent

- and prolonged periods of moisture stress projected for the region (Coats et al. 2013),
- notwithstanding the potential for more climate-disturbance feedbacks (Loudermilk et al. 2013).

Conclusions

over large areas, but this is often coupled with biotic triggers of insect outbreaks that induce

407 mortality and shift community composition at sub-regional scales. Deconstructing the relative

408 contributions of each Our cross-scale comparison demonstrates that representing the effects of both climate and bark beetles on tree growth produces a high level of agreement between simulated and empirical estimates of ANPP. Furthermore, our forest growth analysis suggests that both climatic and disturbance influences should be considered when estimating or projecting ANPP. The limitations on forest growth at the landscape scale are complex, with biotic and abiotic factors playing unique, yet often confounding roles. Regional climate trends may influence productivity mortality and shift community composition at sub-regional scales. Deconstructing the relative contributions of each of these factors is important for evaluating model robustness, and using the combination of empirical and simulated data improves projections of future forest dynamics. Ecosystem models can capture the effects of these various influences at scales unavailable to most field studies – a critical capacity for projecting growth patterns into the future changing world.

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Page 21 of 98

Canadian Journal of Forest Research

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Figure legends

- Figure 1: Study area map. Dots signify field site locations of tree core sampling; the orange area
- represents LANDIS-II modeling extent; the grey area is the entire Lake Tahoe Basin.
- Figure 2: Temperature and average annual precipitation for the Lake Tahoe Basin for the study
- period of 1986-2007. Temperature and precipitation data were estimated by 4km Parameter-
- elevation Relationships on Independent Slopes Model (PRISM) data, averaged across 18 tiles;
- Climatic water deficit (CWD) data is the average of the Basin Characterization Model (BCM)
- tiles. Average annual precipitation is average total precipitation for calendar year. Dotted lines
- above and below-average temperature represent average annual maximum temperature and
- average annual minimum temperature.
- Figure 3: Conceptual diagram of LANDIS-II.
- DIS-II.
PP data with four L. Figure 4: Comparison of empirical ANPP data with four LANDIS-II model scenarios: 'LowM-
- noBB' (low moisture sensitivity, no bark beetle outbreaks), 'LowM-BB' (low moisture
- sensitivity, bark beetle outbreaks), 'HiM-noBB' (high moisture sensitivity, no bark beetle
- outbreaks), and 'HiM-BB' (high moisture sensitivity, bark beetle outbreaks). Each line
- represents the median ANPP (tree ring n=52, LANDIS-II scenarios n=31,291), shaded areas
- around each median line represent bootstrapped 95% confidence intervals, 500 draws each.
- Figure 5: Median ANPP as a function of average annual climatic water deficit (CWD), as calculated by
- the Basin Characterization Model. Regression lines show distinction between moisture sensitivity at low
- moisture stress levels (low CWD) and high moisture stress levels (high CWD).

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Tree ring IowM-noBB lowM-BB hiM-noBB hiM-BB 300 Median ANPP $(g C m^{-2})$ **Draft** 100 **https://mc06.manuscriptcentral.com/cjfr-pubs** 1990 2005

ANPP Response to Moisture Availability

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Table S1: Plot metadata including plot location, topography and forest type for 21 sampled drainage creeks across the Lake Tahoe Baisn.

Table S2: Tree ring summary statistics

ABCO												
	series	first	last	year	mean	median	stdev	skew	sens1	sens2	gini	ar1
1	BC01A1	162	271	110	3.081	2.987	0.884	0.095	0.188	0.175	0.156	0.615
$\overline{2}$	BC01A3	196	271	76	1.531	1.442	0.785	1.621	0.295	0.332	0.259	0.311
3	BC01A6	171	271	101	3.702	3.46	1.774	1.564	0.162	0.155	0.251	0.734
$\overline{\mathbf{4}}$	BC02A7	181	271	91	1.825	1.883	0.8	-0.198	0.233	0.202	0.251	0.79
5	BC02A10	99	271	173	2.096	2.062	0.636	0.426	0.187	0.174	0.168	0.724
6	BLC02A2	204	271	68	1.792	1.611	0.82	1.671	0.211	0.207	0.226	0.712
7	BLK01A1	200	271	72	4.098	4.192	1.058	0.201	0.136	0.132	0.146	0.764
8	BLK02A5	216	271	56	4.328	4.044	1.711	0.282	0.156	0.154	0.224	0.836
9	BLK02A4	167	271	105	2.302	2.424	0.734	-0.21	0.167	0.157	0.181	0.738
10	BLK02A2	207	271	65	3.161	3.25	0.586	-0.218	0.159	0.153	0.104	0.498
11	BLK02A1	230	271	42	2.335	2.307	0.349	0.276	0.135	0.136	0.084	0.315
12	BLK02A3	184	271	88	1.857	1.886	0.871	0.006	0.182	0.159	0.268	0.855
13	BLK03A2	191	271	81	3.505	3.088	1.854	2.122	0.153	0.162	0.246	0.889
14	BLK03A8	160	271	112	2.641	2.74	1.196	0.643	0.141	0.138	0.25	0.809
15	BLK03A7	199	271	73	2.677	2.216	1.425	1.578	0.18	0.174	0.275	0.74
16	BUI01A5	173	271	99	2.008	1.868	1.069	1.453	0.207	0.182	0.273	0.773
17	BUI02A2	200	271	72	2.195	2.243	0.775	0.158	0.211	0.189	0.2	0.717
18	DC01A1	203	271	69	2.645	2.769	0.805	-0.005	0.231	0.219	0.171	0.553
19	DC01A7	131	271	141	2.728	2.759	1.514	0.131	0.186	0.144	0.318	0.938
20	DC02A3	176	271	96	1.368	1.385	0.396	0.179	0.195	0.188	0.163	0.547
21	DC02A4	198	271	74	1.786	1.869	0.423	-0.687	0.187	0.167	0.128	0.523
22	GC01A1	119	271	153	0.721	0.422	0.66	1.273	0.209	0.185	0.479	0.941
23	GC01A3	205	271	67	1.512	1.395	0.69	0.446	0.226	0.211	0.257	0.814
24	GC03A2	205	271	67	2.809	2.744	0.943	0.042	0.206	0.19	0.19	0.725
25	GC03A4	144	271	128	2.712	2.794	1.079	-0.215	0.153	0.141	0.225	0.87

Table S3: Sample size of cored trees by species, segregated by East and West side of the Lake Tahoe Basin.

Table S4: Pearson correlation coefficients used for annual increment core data

See attached supplemental file TableS4_CorrCoeff.xlsx

Table S5: Mean live tree basal area $(m^2 \text{ ha}^{-1})$ by species by site for inventory plots. Orientation, East (E) and West (W) side of the Lake Tahoe Basin, is denoted for each site. Species codes are as follows: *Abies concolor* (ABCO), *A. magnifica* (ABMA), *Calocedrus decurrens* (CADE), *Pinus jeffreyi* (PIJE), *Pinus lambertiana* (PILA).

Table S6: Mean dead tree basal area $(m^2 \text{ ha}^{-1})$ by species by site for inventory plots. Orientation, East (E) and West (W) side of the Lake Tahoe Basin, is denoted for each site. Species codes are as follows: *Abies concolor* (ABCO), *A. magnifica* (ABMA), *Calocedrus decurrens* (CADE), *Pinus jeffreyi* (PIJE), *Pinus lambertiana* (PILA).

 LANDIS-II. Species codes are consistent with previous supplemental tables, with the following additional codes: *P. albicaulis* (PIAL), *P. contorta*(PICO), *P. monticola* (PIMO), *C. decurrens* (CADE),

Table S8: Linear regression models of ANPP ~ CWD for both high CWD and low CWD levels for tree ring-estaimted ANPP and all LANDIS-II model scenarios. Low CWD indicates all CWD values below 41mm, the determined break point in the linear regression.

Model Parameterization

Century Succession extension

Draft
Iodgepole pine, white fir, red fir, incense cedar, and mountain hemlock. The 'hardwood
tremuloides). The 'shrub' group consisted of four generic shrub types, Non N-fixing ob
resprouting shrubs, N-fixing obligate Carbon dynamics were modeled using the Century Succession extension ('*Century*') for LANDIS-II, which is based on the CENTURY soil model (Parton et al. 1983). *Century* was calibrated and validated with available data to satisfy five model output targets: aboveground net primary productivity (ANPP), Net Ecosystem Production (NEP), aboveground live biomass, soil organic C (SOC), and soil inorganic nitrogen (mineral N) (Loudermilk et al. 2013). Further details on model development, parameterization, and calibration are in Loudermilk et al. (2013). Our simulations contained three functional groups (conifers, hardwoods, and shrubs) of which the conifers were most abundant. The 'conifer' group contained Jeffrey pine, sugar pine, whitebark pine, western white pine, lodgepole pine, white fir, red fir, incense cedar, and mountain hemlock. The 'hardwood' group consisted of quaking aspen (*Populus tremuloides*). The 'shrub' group consisted of four generic shrub types, Non N-fixing obligate seeding shrubs, Non N-fixing

Century utilizes monthly climate data, which influences tree establishment, growth, and regeneration (Scheller et al. 2011). Individual species' growth response to available soil moisture is dictated by two parameters; these parameters are assigned to broader functional groups to which each species belongs. These two parameters dictate moisture sensitivity by determining the ratio of available water content (AWC) to potential evapotranspiration (PET). The first parameter ('DroughtIntercept', in CENTURY: 'pprpts2') determines the effect of AWC on the intercept of this relationship, therefore if this value is increased, the intercept is raised and higher AWC is required to achieve the same PET. The second parameter ('DroughtRatio', in CENTURY: 'pprpts3') is the minimum ratio of AWC/PET at which there is no restriction on production, effectively determining the minimum AWC necessary for any growth to

occur. The LANDIS-II *Century* extension requires calibration of these moisture-related parameters to accommodate unique species and soils combinations.

bration targets in Loud

e and the scenarios we

eetles (LowM-BB), high We simulated two levels of tree moisture sensitivity and two levels of bark beetle occurrence (with and without bark beetles, extension discussed below). We developed two levels of moisture sensitivity (low and high) by leaving DroughtIntercept constant and iteratively increasing the DroughtRatio parameter by the minimum amount (0.1) demonstrated to have a significant effect on the response variable (ANPP) because this parameter is not empirically derived. 'Significant effect' in this context is defined as 50% increase or reduction in ANPP, well above the tolerance of the calibration targets in Loudermilk et al (2013). We simulated both levels of DroughtRatio with both levels of bark beetle occurrence and the scenarios were named as follows: low moisture sensitivity with no beetles (LowM-noBB), low moisture sensitivity with beetles (LowM-BB), high moisture sensitivity with no beetles (HiM-noBB), and high moisture sensitivity with beetles (HiM-BB).

Using LANDIS-II, we ran five replicate 20-year simulations of each scenario for the 31,000 ha study area using a 100m x 100m grid and climate data from 1987-2006. Monthly temperature and precipitation values for 1987-2006 were from the PRISM dataset for the LTB, at a 4km resolution (18 PRISM tiles total across the study area). Although forest thinning operations and wildfires occurred in the LTB during 1987-2006 timeframe, there were no records or physical evidence of any recent fire (wildfire or prescribed burning) or thinning at the field locations where tree-cores were collected. We excluded these disturbances from out simulations to be congruent with field site disturbance history over the study period.

BDA parametrization extension

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 Draft Three bark beetle species were modeled: the Jeffrey Pine Beetle ('JPB'), the Mountain Pine Beetle (*Dendroctonus ponderosae,* 'MPB'), and the Fir Engraver Beetle (*Scolytus ventralis,* 'FEB'). Although there are other beetles active in the area (e.g. Red turpentine beetle (*Dendrocotnus valens*), these three beetles are responsible for the majority of the recorded damage in the LTB and there is very little overlap in host species. Empirical data from the literature and expert opinion were used to determine host species and ages most preferred by each of the three modeled beetle species (Table S7). JPB and FEB are limited in their primary host selection (Jeffrey pine and red/white fir respectively), whereas MPB is more of a generalist, impacting a variety of pine species across the basin (Cole and Amman 1980; Ferrell 1994; Bradley and Tueller 2001; Walker et al. 2007; Egan et al. 2010). Beetle dispersal is modeled within BDA, defined at an annual rate $(m \text{ year}^{-1})$.

A widespread outbreak of bark beetles occurred in the region, concurrent with a severe drought that began in 1988. USFS Aerial Detection Survey (ADS) maps of the basin indicated >15,000 ha of damaged area during the peak year of the outbreak (1993). ADS maps include attribution of damage to specific beetle species on an annual basis, allowing us to use these survey data to calibrate each of the three beetle species modeled in this study. Total forest area impacted over the study period for each beetle species was 15,785 ha: mountain pine beetle (933 ha), Jeffrey pine beetle (3126 ha), and Fir engraver beetle (11726 ha).

Outbreaks are probabilistic at the site level, where the probability of a site being disturbed is based on the available hosts within site as well as neighboring resources (hosts). Individual host tree species are ranked (primary, secondary, minor, and non-host) and described

Draft correction for two reasons; firstly, fir engravers are typically less aggressive (i.e., lower mortality percentage amongst affected stands) correction for two reasons; firstly, fir engravers are typically less aggres by both species and age. In the LTB, the Jeffrey pine beetle (*Dendroctonus jeffreyi*) is an obligate of Jeffrey pine, though it prefersolder cohorts (>60 years, primary host) much more than younger cohorts (<20 years old, minor host) (Egan et al., 2010). These host categorizations help determine 'site vulnerability' (Sturtevant et al., 2004). The severity of a simulated outbreak is a function of site vulnerability, classified as light, moderate, and severe. A 'light' outbreak kills all vulnerable cohorts; a 'moderate' outbreak kills all tolerant and vulnerable cohorts; and a 'severe' outbreak kills resistant, tolerant, and vulnerable cohorts. Outbreaks are synchronous across a landscape, and severity can be bounded by defining a minimum and maximum possible outbreak severity. The BDA extension reduces site and landscape ANPP through mortality of affected cohorts rather than direct reductions in cohort growth rates. Total forest area impacted over the study period for each beetle species was: mountain pine beetle (933 ha), Jeffrey pine beetle (3126 ha), and Fir engraver beetle (11726 ha). From the ADS flyover maps and expert opinion, total area affected by FEB required modest than species of genus *Dendroctonus*, killing fewer trees per hectare*.*

Because mortality within the BDA extension removes entire species/age cohorts on a given site rather than individual trees, this might lead to an overestimation of mortality of FEB hosts on affected sites. Secondly, FEB are generally restricted to areas dominated by their host species. Thus, areas defined as impacted by FEB on ADS maps may have overstated the total area affected by FEB because the full extent of all mapped FEB areas was not entirely fir-dominated. To correct for this overestimation, stand dominance by tree species was determined using biomass estimates within a 5 ha moving window across modeled sites. Stands that contained >75% red and white fir and were within an identified outbreak zone were determined to have likely been impacted, which could then be totaled

to calculate total area affected by Fir Engraver. This correction factor was not applied to area affected by the two species of *Dendroctonus* beetles, as the flyover maps were reasonable estimates of damage. Therefore, area affected by each beetle species was calibrated to reproduce the following: mountain pine beetle (933 ha), Jeffrey pine beetle (3126 ha), and fir engraver (8795 ha). Total area affected in the peak outbreak year of 1993 within the model was 10,418 ha, compared to remotely sensed estimates of 15,783 ha. Mortality from beetle outbreaks within our simulations began 3 years after the severe drought event in 1988 and lasted for 7 years; a period which matches flyover maps and local opinion (USDA Forest Service Pacific Southwest Region 2013).

Supplemental References

Region 5 Aerial Detected Section 2012. USDA Forest Service Pacific Southwest Region. 2013. Region 5 Aerial Detection Monitoring. http://www.fs.usda.gov/detail/r5/forestgrasslandhealth/?cid=fsbdev3_046696. Accessed October 2012.

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