

Spruce beetle outbreak was not driven by drought stress: evidence from a tree-ring iso-demographic approach indicate temperatures were more important

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May 5, 2020

Abstract

Climate change has amplified eruptive bark beetle outbreaks over recent decades. However, for projecting future bark beetle dynamics there is a critical lack of evidence to differentiate how outbreaks have been promoted by direct effects of warmer temperatures on beetle life cycles vs indirect effects of drought on host susceptibility. To diagnose whether drought-induced host-weakening was important to beetle attack success we used tree death date demography during a spruce beetle outbreak to differentiate early and late-dying trees and then determined whether early-dying trees had greater sensitivity of tree-ring carbon isotope discrimination to drought. Drought-sensitivity did not differ among early- vs late-dying trees, suggesting proposed links between spruce beetle outbreaks and drought primarily reflect warming- amplified beetle life cycles rather than drought-weakened host defenses. Additional iso-demographic studies are needed to diagnose the role of direct vs indirect climate effects across wider regions and other species.

Introduction

Bark beetles are important agents of forest disturbance that are influenced by climate change in ways that are expected, in most cases, to cause outbreaks to be more frequent, severe or move into new regions (Berg et al. 2006; Raffa et al. 2008, Bentz et al. 2010). Recent climate change, including warmer, drier conditions throughout much of the range of *Picea engelmannii* (Easterling et al. 2000; Rehfeldt et al. 2006; Seager et al. 2007) are thought to have escalated *Dendroctonus rufipennis* populations from endemic to outbreak (DeRose and Long 2007, 2012a). Drought conditions have continued to be linked with recent *D. rufipennis* outbreaks (Hart et al. 2014a, 2017). However, the mechanistic underpinnings of why bark beetle populations tend to transition from endemic to outbreak during drought conditions is lacking for most species of bark beetles.

D. rufipennis outbreaks may be influenced both directly and indirectly by climate (Fig. 1). During the transition from endemic to outbreak beetle population levels, warmer winter and summer temperatures promote an amplified lifecycle; beetles reproduce sooner and more often (Fig. 1; Hansen et al. 2001; Hansen and Bentz 2003; Raffa et al. 2008). Moreover, as long as beetles do not lack for cold-hardening, they are expected to have larger broods due to increased overwinter survival (Massey and Wygant 1954; Bentz et al. 2010). Indirect effects of climate on bark beetle outbreaks are thought to include drought stress that increases susceptibility of host trees that have less non-structural carbon available for inducible defenses (Fig. 1; Raffa and Berryman 1983; Waring and Pitman 1985; Herms and Mattson 1992; Coops et al. 2009; Bentz et al. 2010; Anderegg et al. 2015). Indeed, tree vigor, often interacting with tree size, is important for determining tree susceptibility to *D. rufipennis* (Massey and Wygant 1954; Hard 1983, 1985; Holsten 1984;

Doak 2004). Two intensive experiments have demonstrated how drought can weaken trees and make them more susceptible to bark beetle attack (Gaylord et al. 2013; Kolb et al. 2019) but these findings may not simply translate to endemic beetle populations transitioning to incipient or full irruptive outbreak conditions across landscapes, and to other bark beetle and host species.

Retrospective tree-ring studies can help decipher landscape-level influences on beetle outbreaks and have linked regional droughts to *D. rufipennis* outbreaks (DeRose and Long 2012a; Hart et al. 2014a). In these studies, meteorological droughts were associated with warmer temperatures, reduced snowpack, and longer growing seasons (Winchell et al. 2016; Pederson et al. 2011; Williams et al. 2013; Diffenbaugh et al. 2015; Belmecheri et al. 2016). Due to the covariance of warmer temperatures and drought conditions, bark beetle populations could have been impacted directly by life-cycle amplification during a drought without hosts experiencing drought stress that significantly impacted their ability to marshal resin and other chemical defenses used to ward off bark beetle attacks (Fig. 1). Indeed, *P. engelmannii* growing at high elevation are exposed to summer temperatures that are much cooler and, in many locations, summer monsoon or convective rainfall is more common when compared to the middle- or low-elevation forests. It is exactly these low-elevation trees that are sought in sampling to reconstruct past regional droughts (Williams et al. 2013). Overall, experimental studies provide mechanistic knowledge and retrospective studies have provided patterns linking drought to bark beetle outbreaks. However, it remains unclear whether past *D. rufipennis* outbreaks were directly driven by warmer temperatures with little role for host resistance, or whether drought conditions have played a role in altering host physiology to the extent that resistance to beetle attacks was compromised (Fig. 1).

Tree-ring carbon isotope discrimination ($\delta^{13}\text{C}$) can often provide unique insights on drought stress among trees and across landscapes. In areas with abundant growing season sunlight, tree-ring $\delta^{13}\text{C}$ records the degree to which stomatal conductance constrains canopy-integrated leaf gas exchange, which in turn records a shorter-term atmospheric water deficits and longer-term soil moisture deficits integrated across weeks to months in most cases (McCarroll and Loader 2004; Saurer and Voelker 2020). Where soil moisture is abundant in snowy montane forests, tree-ring $\delta^{13}\text{C}$ primarily records summer drought stress imposed by past variation in temperatures (Ratcliff et al. 2018). More specific to *D. rufipennis* outbreaks, tree-ring $\delta^{13}\text{C}$ had correlations with temperature that were stronger in beetle-killed *Picea glauca* as compared to surviving conspecifics in Alaska (Csank et al. 2016). Altogether these findings provide support for the use of $\delta^{13}\text{C}$ to provide a canopy-integrated record of past leaf gas exchange responses to summer drought stress.

Most retrospective studies of bark beetle outbreaks have compared various aspects of live and dead trees without regard for when dead trees were attacked and died and/or whether the outbreak was over (McDowell et al. 2010; Knapp et al. 2013; Csank et al. 2016; DeRose et al. 2017), and this could present opportunities or problems for interpreting results. For example, if >95% of overstory trees died during an outbreak, sampling of survivors would represent an extreme tail in the distribution of tree characteristics that could yield insights on how host genetics or physiology impacted beetle outbreaks if the only trees surviving outbreaks had exceptional capacity for defense. However, sampling the <5% of overstory trees that survived may dilute those signals where trees grew in locations where substantial beetle populations did not disperse, and/or microsite conditions benefitted tree defenses. Sampling of the >95% of trees that died during an outbreak would likely include a small proportion of trees that died early and had lower resistance; whereas a much larger proportion would have had stronger resistance, but ultimately not enough to successfully defend against mass attacks during the peak of a bark beetle outbreak. To avoid comparisons that are potentially disparate by way of demography, we developed an iso-demographic approach based on carbon isotope signals and the timing of tree death to contrast trees that died early vs late during an outbreak (Fig. 2; see Appendix S1: Fig. S1 in Supporting Information).

For our *P. engelmannii* system, if host drought stress was an important driver advancing *D. rufipennis* outbreaks, we hypothesized that the drought sensitivity of $\delta^{13}\text{C}$ in early-dying trees should be greater than late-dying trees (Fig. 1). Supported by theory (Herms and Mattson 1992) and evidence that tree vigor was one of the major drivers of past beetle attack success (Massey and Wygant 1954; Hard 1983, 1985; Holsten

1984; Doak 2004), this approach implicitly assumes that early-dying trees, would have had fewer resources to defend themselves relative to tree size, whereas late-dying trees would have had more resources for induced defenses relative to tree size, but were eventually overwhelmed by outbreak beetle populations. In contrast, if the drought sensitivity of $\delta^{13}\text{C}$ were found not to differ among early- and late-dying trees, this would provide evidence that drought stress did not significantly alter host physiology and that the direct effect of temperature on beetle populations was primarily responsible for the transition from endemic levels to an irruptive outbreak. Hence, this study uses a well-characterized *D. rufipennis* outbreak that killed 95% of overstory *P. engelmannii* between ca . 1990 and 2000 (DeRose and Long 2007) to identify early- and late-dying trees and thereafter test the relative influence of drought stress versus warmer temperatures in the development of that outbreak.

Methods

Study site

We used archived increment cores that were collected as part of a study of forest responses to bark beetle attack during the summers of 2005-2007 on the Markagunt Plateau in southern Utah, located on the western edge of the Colorado Plateau (see DeRose and Long 2012a, 2012b; Table 1, Fig. 3). Prior to a *D. rufipennis* outbreak in the 1990s that killed over ninety-five percent of overstory *P. engelmannii* (DeRose and Long 2007; DeRose et al. 2017), these forests were dominated by *P. engelmannii* and *Abies lasiocarpa* and included smaller components of *Populus tremuloides* or *Pseudotsuga menziesii* (Appendix S1: Fig. S2). Our six study sites were distributed across the plateau, ranged in elevation from 3202 to 2879 m, and ranged in pre-outbreak *P. engelmannii* basal area from 91.3% to 55.5% (Appendix S1: Table S1). Plots were located in areas representative of the larger forest matrix where trees were killed that spanned all slopes and aspects across the plateau.

Increment core preparation for stable isotope analyses

Six sites were chosen for further analyses based on the abundance and quality of the increment cores. The date of last year of growth was verified for every core using visual crossdating and COFECHA software (Holmes 1983; Yamaguchi 1991). Cross-dated cores were used to identify the last year of growth which indicated when the tree died. The resulting distribution of death years identified trees that died early, when beetle population levels were building, or later during outbreak population levels (Fig. 2; Appendix S1: Fig. S1). Specifically, early- and late-dying trees were identified as those that died during years occupying the respective tails of the death-year distribution within each stand, after excluding outliers that may have died previous to significant beetle activity (Pettit 2018; Appendix S1: Fig. S1). Cores earmarked for stable isotope analyses were re-measured to include earlywood- and latewood-specific growth back to 1930 using a Velmex measuring system. Annual basal area increment (BAI) was calculated for each tree from the outside toward the pith assuming estimates of the diameter inside the bark from the diameter outside the bark (Myers and Alexander 1972), and by estimating areal growth from annual rings could be generalized as concentric circles. Trees identified for stable isotope analyses were determined on a site-by-site basis to obtain the greatest separation of early- and late-dying trees that included at least five dead trees within each group, and to ensure a large enough sample mass for stable isotope analyses (Table 1; Appendix S1: Fig. S1).

We composited the latewood of tree-rings across a site and within timing categories (i.e., each site had two sets of samples for each year that were distinguished by trees that died early versus late). Compositing rings by year for stable isotope analyses assures sufficient cellulose for stable isotope analyses when rings of trees are very small (e.g., Tardif et al. 2008; Voelker et al. 2014; Csank et al. 2016; Ratcliff et al. 2018) and typically yields an expressed population signal greater than 0.85 (Leavitt 2010). Latewood was excised from each ring to better isolate moisture stress during the summer months (Parker and Henoeh 1971; Faulstich et al. 2013). Wood was ground to a coarse powder using a Wiley mill before extracting to holocellulose (Leavitt and Danzer 1993), homogenized using a 500-W ultrasonic probe (Laumer et al. 2009), and weighed into tin capsules on a microbalance. Samples were analyzed on a Thermo Delta V Advantage

isotope ratio mass spectrometer at the Newell Stable Isotope Laboratory located at Utah State University (http://www.usu.edu/geo/newell/Newell_Website/Stable_Isotope_Lab.html). Carbon isotope composition, is expressed using “delta” notation as $\delta^{13}\text{C} = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$, where $\delta^{13}\text{C}$ is the molar ratio of heavy to light isotopes and R_{standard} is Vienna Pee Dee Belemnite (VPDB). Precision across replicate ^{13}C analyses of cellulose was $1\sigma = 0.12$ ‰ for all sites to include a common period of at least three decades of inter-annual climatic variability leading up to the *D. rufipennis* outbreak. Following Farquhar et al. (1989), cellulose $\delta^{13}\text{C}$ data were converted to $\Delta^{13}\text{C}$ as: $\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{plant}}) / (1 + \delta^{13}\text{C}_{\text{plant}} / 1000)$, where $\delta^{13}\text{C}_{\text{air}}$ values for each year followed those given in McCarroll and Loader (2004).

Drought sensitivity assessment

To determine if the climate sensitivity of $[\delta^{13}\text{C}]$ varied between the trees that died early versus late in the outbreak, we used both a hypothesis testing and model comparison approach. For both, we conducted linear mixed-effects modeling with repeated-measures that also accounted for the nested design of early- and late-dying trees per site. The repeated measurement was raw $[\delta^{13}\text{C}]$ with a first order autoregressive residual covariance structure to account for temporal autocorrelation. For the hypothesis testing approach, we tested $[\delta^{13}\text{C}]$ responses with an interaction between the most influential climate variable (see below) and timing of death (early or late) where the presence or absence of a significant interaction would determine the importance of drought-sensitivity during the progression of beetle outbreaks. For the model comparison approach, we examined three competing models using Akaike information criterion (AIC) and likelihood ratio tests (Burnham and Anderson 2002). The first model assumed no difference in the climate sensitivity of early- vs late-dying trees, the second included an intercept effect of timing of death (early vs late) in addition to climate, and the third, included an interaction between timing of death and climate. Regression analyses were conducted using the “nlme” and “visreg” packages in R (R Core Team 2016; Breheny and Burchett 2017; Pinheiro et al. 2017). Before assessing the influence of host drought stress in driving beetle outbreaks, we first identified which metrics and months best captured drought stress at our sites by calculating correlations between monthly and seasonally resolved climate variables calculated from Climate WNA (Wang et al. 2016) and tree-ring variables (Appendix S1; Table S2). Variables of interest included climatic moisture deficit (CMD) defined as precipitation minus reference evapotranspiration for June, July, and August (after the Hargreaves method, Yates and Strzepek 1994), temperature, water year precipitation (previous October to current September), and the Palmer Drought Severity Index (PDSI, Palmer 1965; Guttman and Quayle 1996).

Predicting date-of-death

We predicted timing of death of trees as a secondary metric to assess the importance of drought stress in driving beetle outbreaks by including metrics related to tree size, vigor, and drought stress. Predictions of date-of-death were conducted at the tree-level. More specifically, tests of date-of-death used annually resolved $[\delta^{13}\text{C}]$ data averaged across all the trees by site, and by time of death, whereas tree size (DBH) and growth rate (BAI) data were used on the individual tree-level. $[\delta^{13}\text{C}]$ values for each site and timing category were applied to all trees within the site (e.g., all early-dying trees at the ASH site were given the same $[\delta^{13}\text{C}]$ value for a given year). Similar to the temporal resolution of $[\delta^{13}\text{C}]$, annual BAI values matching the timeframe of $[\delta^{13}\text{C}]$ (1960-death) were used. A linear mixed effects model was used to predict date-of-death per tree. Due to the variability among plots, date-of-death was calculated as the number of years from the year of peak mortality by site (positive values indicate years of survival post peak mortality, and negative values, years prior to the peak mortality that trees died, Table 1). The model was fitted with all hypothesized main effects (BAI, DBH, $[\delta^{13}\text{C}]$, and their interactions) and interpreted in terms of significance at $p < 0.05$. Random effects were used to account for the nested nature of years repeated for trees within sites. All analyses were done using the “nlme” and “visreg” packages in R (R Core Team 2016; Breheny and Burchett 2017; Pinheiro et al. 2017).

Results

$[\delta^{13}\text{C}]$ chronologies averaged across early- and late-dying trees from all sites were correlated with summer

(i.e., June, July and August) monthly maximum temperatures, climatic moisture deficit (CMD), water year precipitation, and Palmer Drought Severity Index, and averaged -0.38, -0.44, 0.26, and 0.36, respectively, (Appendix S1: Table S2). In contrast, ring width, latewood width, and earlywood width chronologies had correlations with the same climate variables that were near zero (Appendix S1: Table S2). As expected, the slopes of $[\delta^{13}\text{C}]$ versus summer CMD were generally negative for early- or late-dying trees at each site. Because $[\delta^{13}\text{C}]$ was most highly correlated to CMD when compared to other climate variables (Appendix S1: Table S2), subsequent tests of drought sensitivity were defined as the slope of $[\delta^{13}\text{C}]$ vs summer CMD.

Models that assessed drought sensitivity revealed no significant difference between timing of death (early or late mortality during the beetle outbreak at each stand) regardless of which approach was used (hypothesis testing or model comparison). The slopes of $[\delta^{13}\text{C}]$ vs CMD, which reflected the drought sensitivity of leaf gas exchange, were very similar between early- and late-dying trees and did not differ significantly (Table 1; Fig. 4; Appendix S1: Table S3). These overall patterns reflected greater variation in slopes of $[\delta^{13}\text{C}]$ vs CMD among sites for late-dying trees, and the extent to which the variation in drought sensitivity for late-dying trees overlapped with the slopes of early-dying trees was consistent among sites (Fig. 5).

The only evidence we found for differential susceptibility of early- vs late-dying trees to drought stress was when tests were performed on years including only the top 66 percentile of CMD, or the warmest and driest years in the dataset. Moreover, these differences in the sensitivity of responses of $\Delta^{13}\text{C}$ to variation in CMD were only apparent when a three-way interaction of CMD, timing of death, and the arithmetic mean tree diameter (DBH) of the early/late-dying trees was included (see Appendix S1 for full model methods and results). Without accounting for DBH in the model, drought sensitivity did not differ between early/late-dying trees even in the warmest, driest years (Appendix S1: Table S4, Appendix S1: Fig. S3). In an attempt to account for the site-specific variability in drought sensitivity (Fig. 5), models of drought sensitivity that included stand structure showed one potentially significant effect of drought sensitivity, depending on stand conditions (Appendix S1: Fig. S4). Sites with a large range in the DBH of late-dying trees—indicative of stands with an abundance of large host trees pre-disturbance, where some died at the beginning of the outbreak but others died later—showed a difference in drought sensitivity based on timing of death, where late-dying trees were less sensitive to drought compared to early-dying ones (Appendix S1: Fig. S4). However, our sites did not encompass the range in stand structural conditions expected across all *P. engelmannii* types, and thus this line of inquiry needs further investigation (see Discussion).

Tree diameter (DBH) was the only factor ($p < 0.05$) found to affect the timing of individual tree death (i.e., years before or after peak death date within a stand; Appendix S1: Fig. S5). As tree size increased, timing of death occurred sooner such that trees with DBH > 57 cm tended to succumb to *D. rufipennis* early in the outbreak, and trees < 57 cm DBH tended to survive longer (Appendix S1: Fig. S5). Growth rates (BAI), and leaf gas exchange ($[\delta^{13}\text{C}]$), nor any other interactions with these variables were significant in affecting timing of death.

Discussion

Temperature and other factors are known to directly impact *D. rufipennis* populations, but little is known of whether and how host drought stress may influence the success of beetle attacks, and whether that fosters a transition between endemic and outbreak phases of population dynamics (Fig. 1). To address whether drought stress modified the timing of tree death during a *D. rufipennis* outbreak, our study specified early- and late-dying trees (Fig. 2) and assessed their drought-sensitivity leading up to the outbreak. Here we documented that the slopes of $[\delta^{13}\text{C}]$ to CMD (i.e., drought sensitivity) did not differ among early- and late-dying trees (Figs. 4 and 5; Appendix S1: Table S3). Therefore, overall, drought stress in *P. engelmannii* was not a significant factor driving *D. rufipennis* populations to transition from endemic levels to outbreak. Conversely, this evidence strongly suggests that the role of warmer temperatures was restricted primarily to direct effects on bark beetle population dynamics that ultimately decimated *P. engelmannii* across the landscape.

Critical review of drought stress vs temperature in driving bark beetle outbreaks

Disentangling the effects of temperature from drought stress on bark beetles has been a difficult task because many investigations into climatic influences on outbreaks have been retrospective and are lacking in direct measurements of tree drought stress (Kolb et al. 2016). Of the many species of bark beetles, only *Ips confusus* and *Dendroctonus brevicomis* unequivocally influence tree susceptibility to attack when drought stress is experimentally induced (Gaylord et al. 2013; Kolb et al. 2019). In contrast to these multivoltine-capable bark beetle species that occupy and kill their hosts within forests that occupy consistently dry growing seasons (Breshears et al. 2005; Raffa et al. 2008; Fettig et al. 2019), *D. rufipennis* hosts occupy cold and wet, montane, boreal and subarctic forests where evidence has clearly demonstrated how temperatures exert strong and direct effects on beetle life cycles (shift from semivoltine to univoltine; Hansen et al. 2001; Hansen and Bentz 2003; DeRose et al. 2013).

During the *D. rufipennis* outbreaks that peaked in the early 1990s across south-central Alaska, Berg et al. (2006) concluded that decades of warmer than average temperatures were directly affecting bark beetle populations, but that the potential for drought to have contributed to the outbreaks could not be ruled out. The outbreak we investigated was characterized in a similar manner to Berg et al. (2006), and it was concluded that periods of regional drought were associated with past *D. rufipennis* outbreaks (DeRose and Long 2012a). However, like most other retrospective studies of bark beetle outbreaks, prior to the instrumental record, DeRose and Long (2012a), had no means to differentiate among how precipitation deficits versus warmer temperatures may have contributed to reconstructions of meteorological drought severity (i.e., PDSI). Additionally, regional tree-ring reconstructions of PDSI across this region can be biased toward sites with greater climate sensitivity (Klesse et al. 2018), which may better reflect mid- to low-elevation forests where cloud cover and precipitation from summer convective storms and/or monsoon rains are lower and less consistent compared to the high elevations that *P. engelmannii* occupies.

D. rufipennis outbreaks identified from documentary records across the southern Rockies of Utah and Colorado have been found to be driven by three sets of variables, listed in order of importance: winter temperatures, late summer and fall temperatures, and annual PDSI (Hebertson and Jenkins 2008). Since PDSI is strongly influenced by temperature (Sheffield et al. 2012), it can be concluded from the results of Hebertson and Jenkins (2008) that the primary cause of *D. rufipennis* outbreaks has been temperature and that there may be indirect evidence for drought stress having had a smaller but detectable influence. It has also been shown that meteorological drought, often in association with the Atlantic Multi-decadal Oscillation (AMO) have induced *D. rufipennis* outbreaks in Colorado (Hart et al. 2014a). However, the evidence is equivocal whether drought stress can be differentiated from temperature effects on outbreaks for that region because precipitation did not show significant effects for any season (i.e., Hart et al. 2014a, Appendix B). In another retrospective study, *D. rufipennis* -killed trees in Alaska had higher correlations between interannual tree-ring $\delta^{13}\text{C}$ and spring and summer temperatures when compared to surviving trees from the same areas, but no differences in precipitation responses were detected (Csank et al. 2016). Similar to the conclusions of Hart et al. (2014a), the results of Csank et al. (2016) fit within the narrative that bark beetles responded to drought, but only to the extent that meteorological drought is a function of water balance driven by precipitation and temperature. However, these results can be viewed through a lens that distinguishes between meteorological drought (see Fig. 1). Indeed, in our study, there was a lack of significant relationships between ring-width growth parameters and various meteorological drought metrics across all of our sites (Appendix S1: Table S2). These results underscore that tree- or stand-level drought stress may be independent or only weakly related to regional meteorological drought conditions for these high elevation spruce forests. Overall, these previous studies indicate that beetle-killed trees were more responsive to temperature than surviving trees, which agrees with our primary conclusion that drought stress played little role in determining patterns of tree mortality.

There may be a distinct role for drought stress in the coldest boreal or montane forests whereby water, still frozen in tree stems or in soils, can limit water transport and photosynthesis and thereby promote susceptibility to *D. rufipennis* attack (Hard 1987; Bowling et al. 2018). However, drought stress caused via this mechanism occurs at local scales related to topographic variation, and therefore cannot explain the large *D. rufipennis* outbreaks that have swept across many *P. engelmannii* landscapes of the Rocky Mountains

in recent decades. Overall, the body of literature on climatic drivers of *D. rufipennis* outbreaks has found ample evidence that outbreaks were associated with periods of prolonged warmer air temperatures that may have been associated with meteorological drought, whereas evidence is absent or of minor importance that host drought stress increased tree or forest susceptibility leading up to or during outbreaks.

Stand structure may mediate drought effects

Although most evidence suggests that surface air temperatures are the predominate influence on *D. rufipennis* dynamics, drought stress should not be dismissed entirely as a determinant in patterns of outbreak initiation and progression at certain scales, particularly when interacting with stand structure. Indeed, a number of other studies on *D. rufipennis* mortality have investigated how certain aspects of stand structure have affected percentage mortality across landscapes (e.g., Doak 2004; Hart et al. 2014b; Bakaj et al. 2016; Temperli et al. 2014). These studies have largely found tree size to be the best predictors of tree mortality, whereas stand structure has been of lesser importance (Bakaj et al. 2016). Our study confirms that large trees tended to die earlier in the outbreak, signaling beetles preferred these large trees (Appendix S1: Fig. S3). From a landscape-level perspective, *D. rufipennis* will encounter stands with a varying amount of large host trees. Once a bark beetle population encounters and occupies a stand, the subsequent timing of death of *P. engelmannii* may be based on tree size or drought-sensitivity that impacts host defenses, but the importance of each will likely depend on the stand characteristics (Goodsman et al. 2018).

Across the six stands we investigated, drought sensitivity was similar among early-dying trees but different in late-dying trees in some of the stands (Fig. 5; Appendix S1). We hypothesize that, in mature stands where there was an abundance of large trees, the difference in timing of death tended to have been determined in part by the sensitivity of $[\delta^{13}\text{C}]$ to drought or in this case CMD (Fig. 5; Appendix S1: Table S5; Appendix S1: Fig. S6). However, in stands comprised of a mix of large and small *P. engelmannii* (Appendix S1: Fig. S6), the large trees preferred by beetles were less abundant, thereby concentrating the intensity of beetle attack, and subsequently overwhelming hosts regardless of differences in drought sensitivity or drought stress among trees. This interpretation would be consistent with previous findings of small trees being attacked later during an outbreak after the large trees have been exhausted (e.g., Massey and Wygant 1954; Holsten 1984; Dymerski et al. 2001). The difference in individual timing of mortality on a site-by-site basis highlights the unique stand-specific progression of *D. rufipennis* outbreaks that cannot be expected to be consistent across a heterogeneous forest landscape. In stands with abundant large trees, drought sensitivity, as it influences tree susceptibility, affects timing of death. However, in stands with fewer large host trees, a limited density of large trees for beetles to choose from causes the best predictor of timing of death to be tree size, consistent with the findings of Temperli et al. (2014) and Bakaj et al. (2016). More extensive research using our iso-demographic approach will be necessary to address whether variability in drought stress across a landscape may lead to initial hot spots of beetle activity. Ideally, this would be paired with a remote sensing approach, such as shown by Hart et al. (2017), as a guide for directing where to establish tree-ring isotope sampling across a landscape.

Prospects for Projecting Beetle Dynamics

Conclusions

The ubiquity of bark beetle outbreaks across western North America and elsewhere in recent decades provides stark evidence that warming temperatures, drought, and bark beetles are having dramatic impacts on forests (Raffa et al. 2008; Bentz et al. 2010; Fettig et al. 2019). Increased research efforts have been called for to provide greater accuracy in projecting the effects of climate change and pest/pathogen interactions on forests (Anderegg et al. 2015) as well as management actions that may mitigate the impact of bark beetles on forest ecosystem functions (Morris et al. 2017). Our iso-demographic approach from sites near the southwestern range edge for both *P. engelmannii* (Fig. 3) and *D. rufipennis*, demonstrate that drought stress played little role in determining the transition between endemic to outbreak beetle populations (Figs. 4 and 5). Therefore, forecasting of *D. rufipennis* outbreaks and attendant *Picea spp.* forest dynamics may be considered a rather straightforward response to temperature (DeRose et al. 2013). On the other hand, if

our iso-demographic methods were to be widely deployed within a framework that could differentiate among stand structures that are most likely to concentrate or mediate beetle attack pressure on large trees, then perhaps drought stress may still prove to be a significant and complicating factor influencing *D. rufipennis* outbreaks (Anderegg et al. 2015). Similarly, if it is a goal to preserve *P. engelmannii* in areas threatened by climate change and increased bark beetles activity, management actions aimed at reducing drought stress are unlikely to directly affect *D. rufipennis* susceptibility. However, management that maintain a diversity of age and size classes of trees (DeRose and Long 2014), including small regenerating trees that are not susceptible to beetle attack, will be essential to keeping this species present on the landscape (e.g., Pettit et al. 2019), and allowing it additional time to adapt to climate change and/or migrate to nearby refugia.

Acknowledgements

We wish to thank Sierra Oxborrow for assistance with lab work for this project, and Dr. Sarah J. Hart for her feedback on the manuscript. We would also like to acknowledge Veronica Magnusson and the Cedar City Ranger District of the Dixie National Forest for continued support of spruce research on the Markagunt Plateau. This project was made possible through funding from the TW Daniel Endowment, and Utah Agricultural Experiment Station awards 1304 and 1305.

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Table 1 Site summary information for the six sites used in isotope analysis broken up by early and late-dying trees. Range and number of years used in isotope analysis per site/timing combination as well as the number of trees and their range in death dates. Comparisons of tree size (i.e., diameter at breast height, DBH), carbon isotope discrimination ($[\delta^{13}\text{C}]$), and correlation between inter-annual variation in $[\delta^{13}\text{C}]$ and climatic moisture deficit (CMD) among sites, for trees that died early versus late in the outbreak. Standard deviation is included in parenthesis for DBH and $[\delta^{13}\text{C}]$. CMD was averaged for June, July and August for inter-annual correlations of $[\delta^{13}\text{C}]$ versus CMD correlations.

Site	Timing of death	Range of death dates	Isotope dates	# of trees	DBH	$[\delta^{13}\text{C}]$	$[\delta^{13}\text{C}]$ vs CMD corr
ASH	early late	1995-1991	1994-1960	13 6	63.7 (13.9)	15.85 (0.67)	-0.599 -0.533
		1998	1998-1960		24.3 (4.3)	15.70 (0.83)	
HCK	early late	1995-1990	1995-1960	13 8	40.3 (8.0)	15.84 (0.65)	-0.669 -0.446
		1998-1997	1997-1960		29.1 (9.0)	15.22 (0.52)	
HPT	early late	1996-1992	1996-1961*	11 5	47.7 (7.0)	15.09 (0.49)	-0.535 -0.049
		2004-2000	2000-1960		34.6 (14.1)	15.27 (0.37)	
MID	early late	1999-1991	1999-1960	10 6	43.3 (18.8)	15.65 (0.49)	-0.568 -0.595
		2002-2001	2001-1960		29.0 (9.0)	15.89 (0.72)	

Site	Timing of death	Range of death dates	Isotope dates	# of trees	DBH	[?] ¹³ C	[?] ¹³ C vs CMD corr
NLS	early late	1998-1991 2006-2001	1997-1960 2001-1960	8 9	58.9 (12.4) 41.3 (7.5)	15.28 (0.78) 15.42 (0.66)	-0.255 -0.431
SNO	early late	1995-1990 2005-2000	1994-1960 2000-1960	11 6	67.7 (17.0) 60.4 (22.7)	15.07 (0.57) 16.22 (0.74)	-0.555 -0.117
ALL	early late	1999-1990 2006-1998	1999-1960 2001-1960	66 40	53.4 (16.7) 36.5 (16.2)	15.47 (0.69) 15.63 (0.75)	-0.73 -0.66

*: outlier in year 1960 removed

Fig. 1 Conceptual diagram of the relationships that possibly influence *D. rufipennis* outbreaks with particular attention to factors that could influence whether drought stress has played a role in weakening tree resistance to beetle attacks. Box colors; purple represents bark beetle population dynamics across a landscape, blue represents factors affecting water supply, pink represents factors affecting water demand, orange represents regional to local factors driving drought stress, green represents ecophysiological characteristics that vary among trees, gray represents stand- site- or microsite-factors that can modify drought stress and/or likelihood of bark beetle host selection, white represents the likelihood of survival or death for a given timestep during a bark beetle outbreak. Relationship directionality is indicated by symbols in arrows. The shading of arrows reflects the degree to which the relationship has been previously demonstrated, with an emphasis on *D. rufipennis* and its hosts across North America; dark arrows are more strongly established and lighter arrows are more weakly established or in some cases simply hypothesized. Specific aspects of this system that our study addresses are given in boldface type.

Footnotes: ¹Macroclimate evaporative demand is influenced primarily by warm season temperatures and secondarily by cool season precipitation and temperature; by their influence on snowpack persistence into spring or summer months. ²Meteorological drought severity is quantified in this study using mean monthly climatic moisture deficit (CMD) across June to August. ³In montane forest of the Rocky Mountains, forest structure can have a strong influence on soil water via snow interception and ablation; or conversely, how the presence of gaps in forests can locally increase snowpack (Hart and Lomas 1979; Hubbart et al. 2015). ⁴Drought stress is quantified in this study by the sensitivity of latewood carbon isotope discrimination to CMD. ⁵Bark beetle populations, including *D. rufipennis*, are influenced by many factors not represented here, but likely the single greatest effect is how growing season temperatures modify the proportion of beetles that can reproduce in 1- vs 2-yr lifecycles; for more details see (Hansen et al. 2001; Hansen and Bentz 2003; Berg et al. 2006; Raffa et al. 2008; Bentz et al. 2010). ⁶Stand structure, in this case, reflects the relative abundance of large trees within a stand that *D. rufipennis* prefer if tree vigor is low enough and/or if beetle populations are high enough to overwhelm tree defenses (Massey and Wygant 1954; Hard 1983, 1985; Doak 2004). ⁷Drought can affect tree resistance to bark beetles through various mechanisms; for more details see Anderegg et al. (2015). ⁸Many traits factor into tree defense; for *P. engelmannii*, the frequency of traumatic resin duct formation appears to be critical for survival (DeRose et al. 2017). ⁹For this study we use the timing of death within a stand as a surrogate for tree/host resistance to bark beetles.

Fig. 2 Conceptual diagram displaying a demographic sampling approach designed to contrast trees that died early during an epidemic (red bars), to those that died late during an outbreak (blue bars). This approach specifically allows for comparisons of early-dying trees that had lower resistance to incipient bark beetles populations (i.e., building from endemic to outbreak), versus late-dying trees from the same stands that resisted pressure by bark beetle attacks for a longer time. If drought stress contributed to the initiation of a beetle outbreak by constraining carbon gain available for defenses, sensitivity to drought stress should be greater in early-dying compared to late-dying trees.

Fig. 3 The six sites where tree cores were collected on the Markagunt Plateau in southern Utah are shown

as yellow circles overlaid on a regional map showing the extent of canopy *P. engelmannii* mortality (red), *P. tremuloides* or mixed *P. tremuloides* -conifer (green) meadows (pink), lava fields and other non-vegetated lands (dark purple and white, respectively) are after DeRose et al. (2011). A broader context for the sampling is shown by maps of climatic moisture deficit (CMD; after Wang et al. 2016) for the period of 1961-1990 (left) and projected for 2050 (right) across the distribution of *P. engelmannii* .

Fig. 4 Predicted relationship between $[\delta^{13}\text{C}]$ values and climatic moisture deficit averaged across June, July, and August (CMD JJA) colored by early/late timing of mortality from repeated measures mixed effects model showing no significant interaction between timing of death (early vs. late) and CMD JJA (model estimate = 0.000268, $p = 0.76$; Appendix S1: Table S4). Dots represent partial residuals with colors indicating the timing of mortality: red dots/line indicate early-dying trees; blue dots/line indicate late-dying trees.

Fig. 5 Visualization of relationship between raw $[\delta^{13}\text{C}]$ values and climatic moisture deficit averaged across June, July, and August (CMD JJA) for the six sampling sites individually (noted by the three letter code at the top of each panel; Table 1). Linear regression lines have been added for ease of interpretation. Dots represent actual data points with colors indicating timing of mortality: red and blue points/linear regression lines represent early- or late-dying trees, respectively. Gray bands represent confidence intervals.

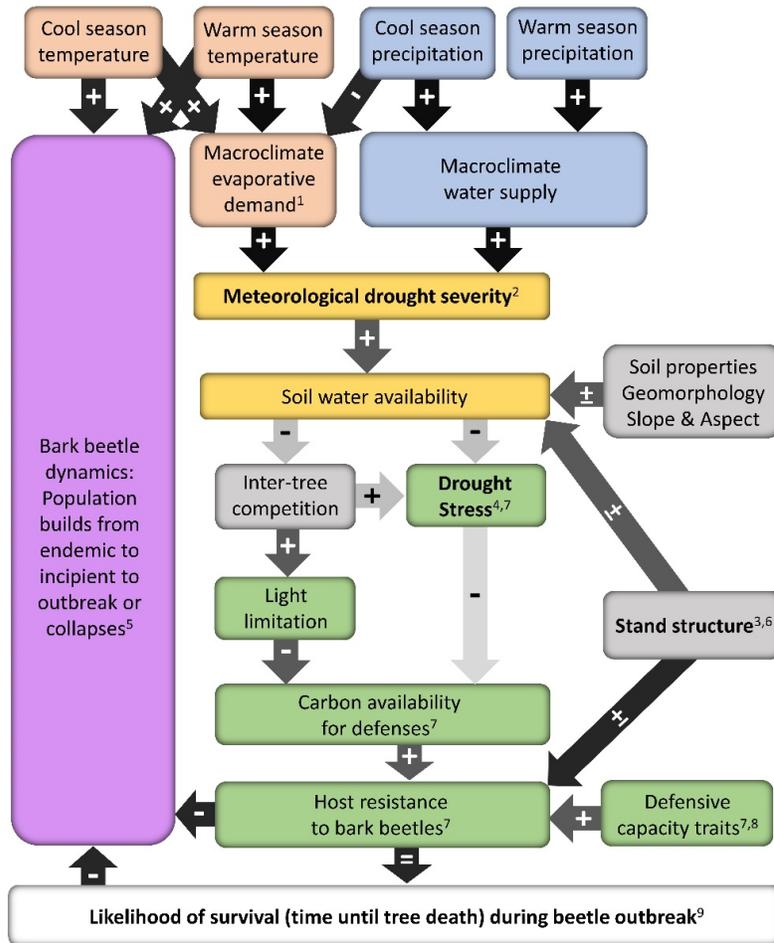


Fig. 1

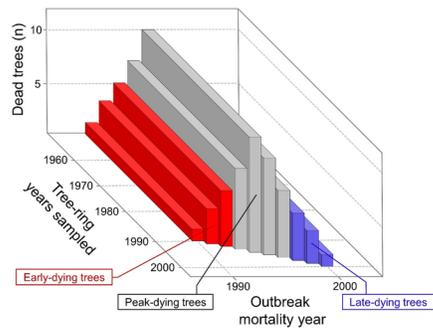


Fig. 2

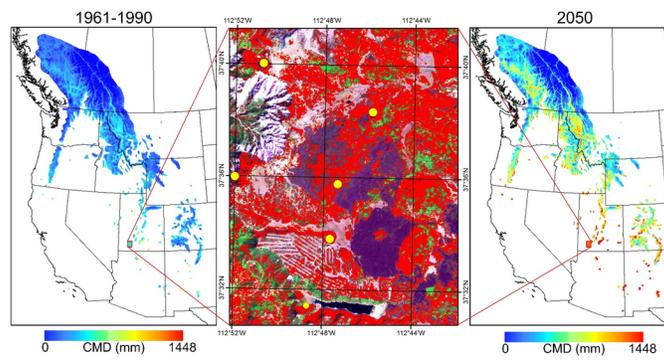


Fig. 3

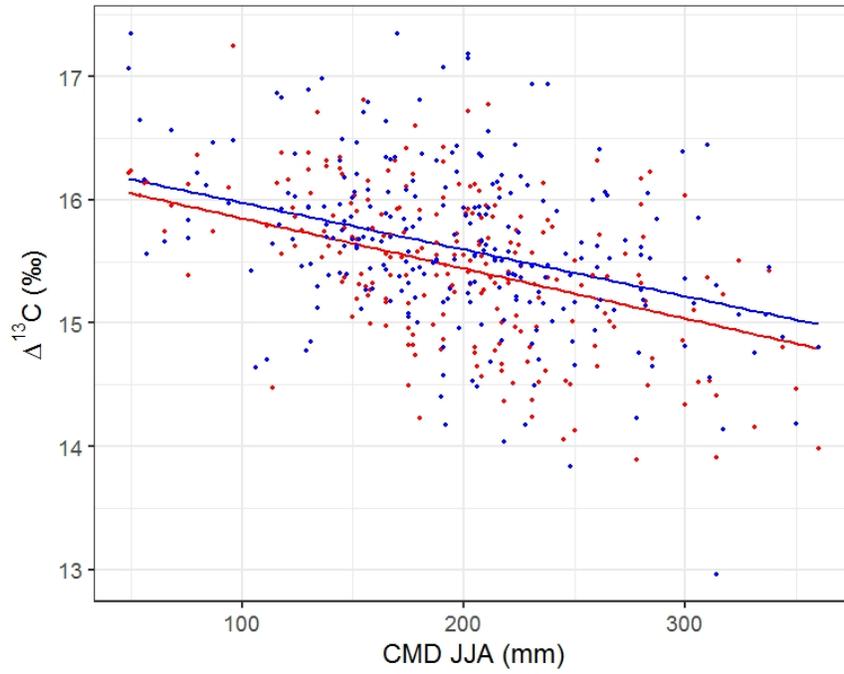


Fig. 4

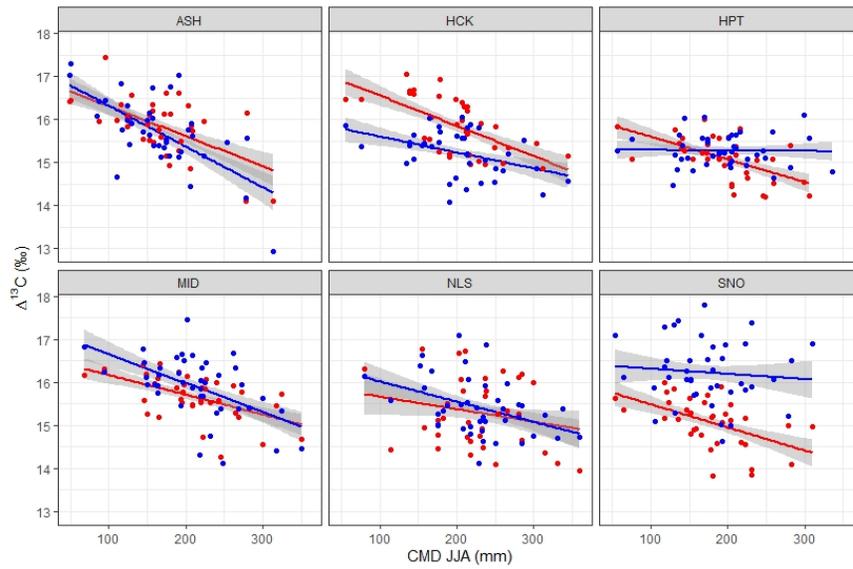


Fig. 5