

Droughty times in mesic places: factors associated with forest mortality vary by scale in a temperate subalpine region

BRIAN J. HARVEY^{1,†}, ROBERT A. ANDRUS², MIKE A. BATTAGLIA³, JOSÉ F. NEGRÓN,³
ALEXANDRA ORREGO,⁴ AND THOMAS T. VEBLEN²

¹School of Environmental & Forest Sciences, University of Washington, Seattle, Washington 98195 USA

²Department of Geography, University of Colorado, Boulder, Colorado 80309 USA

³USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado 80525 USA

⁴Department of Geosciences, Georgia State University, Atlanta, Georgia 30303 USA

Citation: Harvey, B. J., R. A. Andrus, M. A. Battaglia, J. F. Negrón, A. Orrego, and T. T. Veblen. 2021. Droughty times in mesic places: factors associated with forest mortality vary by scale in a temperate subalpine region. *Ecosphere* 12(1): e03318. 10.1002/ecs2.3318

Abstract. Understanding how drivers of ecological disturbance operate across scales is important in an era of increasing disturbance activity. Severe and extensive *Dendroctonus* bark beetle outbreaks across western North America have left in their wake dominance by shade-tolerant and commonly late-seral trees such as subalpine fir (*Abies lasiocarpa*), which can foster resilience of forest cover. However, subalpine fir decline (SFD) is a poorly understood phenomenon that has killed trees across millions of hectares in western North America with unknown consequences for future forest resilience. How different factors (e.g., climate, topography, host-tree characteristics, and abundance) govern SFD presence and severity across spatial scales from individual trees to a subcontinental scale has not been explored in a single framework. Here, we combine broad-scale geospatial data on SFD occurrence, stand-scale field data on SFD severity, and fine-scale individual tree data on mortality to test the relative importance of factors related to SFD across spatial scales spanning >10 orders of magnitude (<1 m to >10 M hectares). At the broadest scale (subcontinental, ~25 M ha), annual areal extent of SFD over time increased sharply with antecedent drought. At regional- (~6 M ha) and stand- (0.1–0.25 ha) scales, the occurrence and severity of SFD were spatially associated with more mesic topographic positions and greater host-tree abundance. Finally, at the individual tree- and tree-neighborhood- (<1 m) scale, the probability of mortality increased for larger trees and trees closer to dead conspecific neighbors. The positive temporal association of SFD with drought at broad scales versus the positive spatial association of SFD with mesic sites at fine scales suggests strong importance of local biotic processes in mediating drought-driven forest decline and highlights the need for understanding multi-scale drivers of ecological disturbance.

Key words: *Abies lasiocarpa*; conifer forest; disturbance ecology; *Dryocetes confusus*; rocky mountains; subalpine fir decline; tree mortality; western balsam bark beetle.

Received 12 March 2020; revised 17 July 2020; accepted 3 August 2020; final version received 10 October 2020.
Corresponding Editor: David Breshears.

Copyright © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† E-mail : bjharvey@uw.edu

INTRODUCTION

Biotic disturbances (e.g., insect and pathogen outbreaks) are integral components of functioning forest ecosystems across temperate zones globally. As the climate warms, biotic disturbances and associated tree mortality are anticipated to increase substantially in area and frequency (Bentz et al. 2010, Allen et al. 2015, Anderegg et al. 2015, Kautz et al. 2017, Seidl et al. 2017). Mechanisms driving biotic disturbances are sensitive to climate conditions and governed by myriad abiotic and biotic drivers and feedbacks operating across a wide range of spatial and temporal scales (Raffa et al. 2008). Such complex interactions across space and time require incorporation of data from a range of scales (Peters et al. 2004, 2011, Falk et al. 2007, Meentemeyer et al. 2012), yet multi-scale analyses are rare (Powers et al. 1999, Seidl et al. 2016, Senf et al. 2017).

Recent outbreaks of bark beetles and associated fungal pathogens have occurred at continental-scale extents across the northern hemisphere (Raffa et al. 2008, Meddens et al. 2012, Lausch et al. 2013, Seidl et al. 2016). For example, subalpine conifer forests in western North America have been recently affected by widespread outbreaks of mountain pine beetle (*Dendroctonus ponderosae*; MPB) and spruce beetle (*Dendroctonus rufipennis*; SB; Raffa et al. 2008, Meddens et al. 2012), which often kill 90% of pine or spruce tree basal area (Simard et al. 2012, Hart and Veblen 2015). The majority of studies on bark beetle outbreaks and fungal pathogen outbreaks from the last several decades has focused on pine or spruce species that are of high economic value. Survival of non-attacked trees is one key mechanism for forest persistence after disturbance (Lloret et al. 2012)—yet, relatively little attention has been paid to biotic disturbances in shade-tolerant and commonly later seral species of lower economic value.

Subalpine fir (*Abies lasiocarpa*) is a key component of forest resilience following recent bark beetle outbreaks in subalpine forests of the Rocky Mountains. Subalpine fir is highly shade tolerant and is characterized by prolific understory establishment in sites dominated by lodgepole pine (*Pinus contorta*) or Engelmann spruce (*Picea engelmannii*; Veblen 1986, Andrus et al.

2018). After MPB- and/or SB-caused death of pine and spruce, respectively, subalpine fir experiences growth release from competition and dominates the recently opened forest canopy (e.g., Veblen et al. 1991, Diskin et al. 2011). Post-outbreak succession to subalpine fir is therefore critical for persistence of subalpine forest ecosystems until future stand-initiating disturbances, although shade-tolerant late-seral species may be particularly vulnerable to stress (Bigler et al. 2007).

From 1994 to 2014, subalpine fir mortality (subalpine fir decline, hereafter SFD) was recorded in over 5 M ha in the western USA (Fig. 1), but the causal mechanisms and consequences for forest resilience are poorly understood. Multiple potentially interacting mechanisms may be responsible for SFD (Lalande et al. 2020). Western balsam bark beetle (*Dryocoetes confusus*; WBBB) is a native insect found throughout the range of subalpine fir that kills trees by excavating galleries in the cambium of older, larger diameter trees with smaller crowns and slower radial growth (Gibson et al. 1997, McMillin et al. 2003, Bleiker et al. 2003, 2005). Two fungal root pathogens caused by *Armillaria* root rot (*Armillaria* spp.) and *Annosus* root disease (*Heterobasidion parviporum*) also infect subalpine fir, causing decay and death to root tissue, predominantly on larger trees (Worrall et al. 2004). Finally, subalpine fir exhibits strongly restricted stomatal conductance during moisture stress (Pataki et al. 2000), making it highly susceptible to mortality during annual and multi-year droughts (Bigler et al. 2007).

Understanding how drivers of tree mortality operate across spatial scales is critical to anticipating future forest disturbance and resilience (Peters et al. 2004, Falk et al. 2007, Meentemeyer et al. 2012). A key knowledge gap in the face of warming temperatures and increasing disturbance is understanding how abiotic and biotic factors can drive patterns of forest mortality—or conversely how these factors can result in refugia for trees from mortality events (McDowell et al. 2019). This understanding is particularly important for understudied, shade tolerant, and commonly late-seral species such as subalpine fir, which are expected to compensate for the tree biomass loss of dominant tree species caused by biotic disturbance (Lloret et al. 2012).

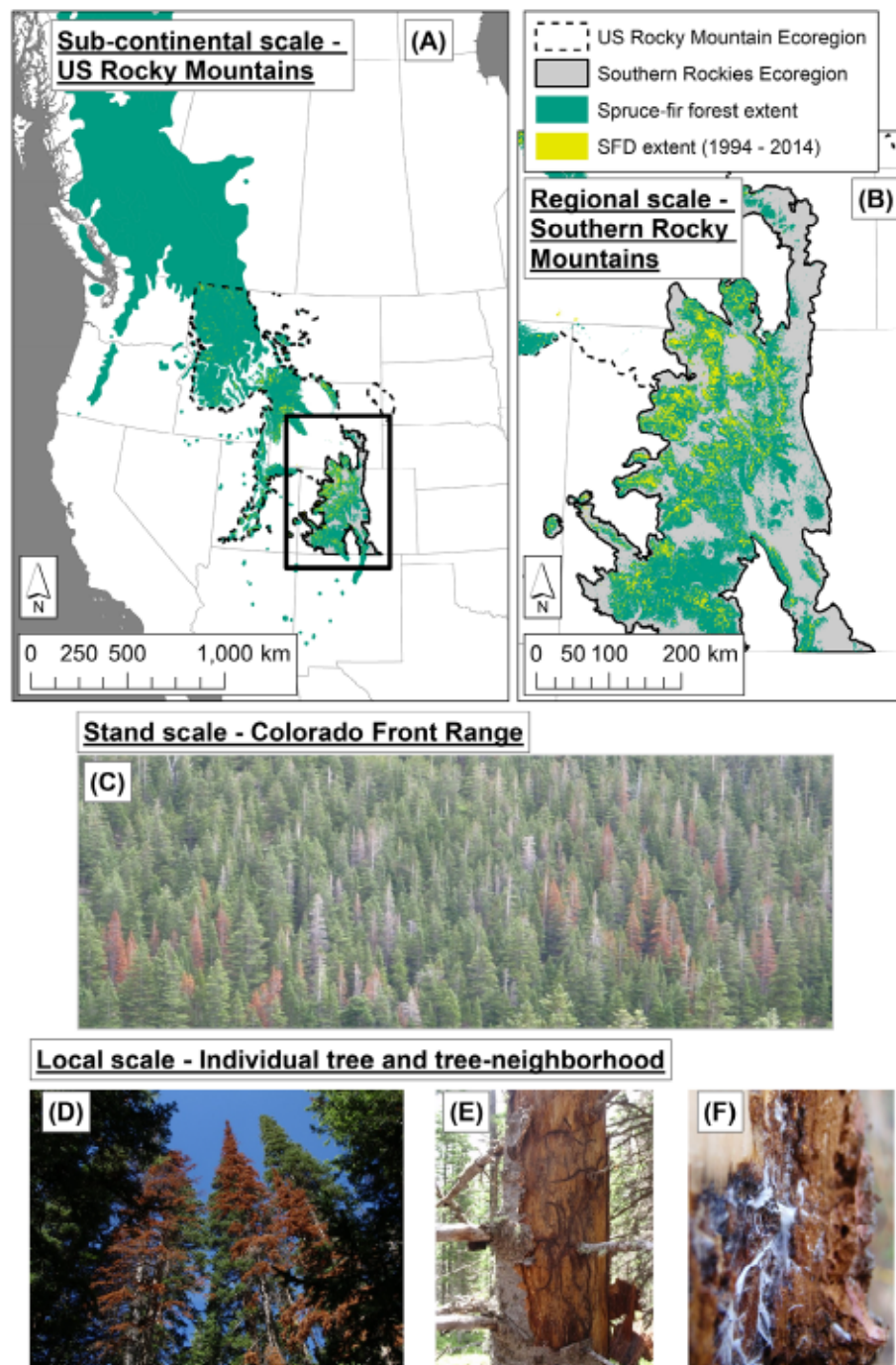


Fig. 1. Spatial scales and examples of subalpine fir decline (SFD) at each scale. Aerial Detection Survey (ADS) data illustrating the spatial extent of SFD (in yellow) at (A) subcontinental and (B) regional scales. Photographs depict SFD severity at (C) stand scales (red and gray tree crowns), as well as (D) individual tree mortality caused by (E) western balsam bark beetle (star shaped galleries under the bark) and (F) *Armillaria* sp. fungus under the bark at the root collar. Photo credits: BJ Harvey.

Table 1. Research questions, spatial scale, and response variables for examining drivers of subalpine fir decline (SFD) across four spatial scales.

Research question	Scale	Extent	Grain	Response variable (source)
1. How is inter-annual variability in SFD extent affected by climate conditions?	Subcontinental	U.S. Rocky Mountains	U.S. Rocky Mountains	Annual area (ha) of SFD occurrence in each year from 1994 to 2014 (ADS data)
2. How is the presence of SFD affected by topography and host-tree abundance?	Regional	Southern Rocky Mountains	26-ha grid cells	Presence/absence of SFD in a grid cell at any point from 1994 to 2014 (ADS data)
3. How is stand-scale severity of SFD affected by topographic context and stand structure?	Stand	Central Colorado Front Range	0.1–0.25-ha field plots	Proportion of subalpine fir basal area in a stand that was dead from SFD (field plots)
4. How is the probability of tree-scale mortality affected by tree size and distance to dead neighbors?	Local: Tree and tree neighbor	0.1-ha plots	Individual trees	Probability of mortality for each subalpine fir tree (field plots)

Note: ADS, Aerial Detection Survey.

We address knowledge gaps introduced above using multiple data sources across spatial scales spanning >10 orders of magnitude to ask four research questions about the fundamental nature of SFD (Table 1). (Q1) How is broad-scale inter-annual variability in SFD extent affected by temporal variability in climate conditions? (Q2) How is regional-scale presence of SFD affected by spatial variability in topography and host-tree abundance? (Q3) How is stand-scale severity of SFD affected by spatial variability in topographic context and stand structure? (Q4) How is local-scale (e.g., tree) probability of mortality affected by tree size and proximity to dead neighbors? For each research question, we tested hypotheses at the appropriate spatial scale about the relative importance of drivers of SFD (Table 2). Among scales, we were interested in how abiotic (e.g., climatic and topographic conditions that are stressful for tree growth and survival) and/or biotic (e.g., higher amount and connectivity of host trees, which can lead to contagious processes of WBBB and fungal pathogens) variables related to SFD occurrence, extent, and/or severity.

METHODS

Study area

At the broadest spatial scale (subcontinental), the study area is the extent of subalpine forest in the U.S. Rocky Mountains (Fig. 1A). We defined the extent of this area using a combination of the EPA level III Ecoregions 15, 16, 17, and 21

(Omernik 1987) and the LANDFIRE Environmental Site Potential (ESP) class Rocky Mountain spruce-fir forests, which corresponds to locations that are dominated by subalpine fir and Engelmann spruce after long periods since a stand-replacing disturbance (Rollins 2009). At the regional scale (southern Rockies), the study area was defined by areas characterized as LANDFIRE Environmental Site Potential (ESP) class Rocky Mountain spruce-fir forests within the Southern Rockies EPA level III Ecoregion 21, which is generally bounded by the coordinates: 37° N to 42° N latitude and 104° W to 109° W longitude (Fig. 1B). At the stand scale, the study area is the central Colorado Front Range east of the continental divide, extending from the Poudre River drainage in the northern portion of Rocky Mountain National Park to the South Boulder Creek Watershed in the Arapahoe-Roosevelt National Forest (ARNF; Fig. 1C). At the finest spatial scale (tree and tree neighborhood), the study area comprises six stem-mapped plots within a subset of field plots (Fig. 1D).

Geospatial and field data sources

Data for the two broadest scales (subcontinental and regional) are from publicly available Geographic Information System (GIS) spatial datasets. We assessed SFD occurrence using the USDA Forest Service Aerial Detection Survey (ADS) dataset (<https://www.fs.fed.us/foresthealth/aviation/aerialsurvey.shtml>), which is produced annually over most forested area in the USA. ADS data are digitized georeferenced

Table 2. Predictor (or candidate for stand-scale) variables for SFD at each spatial scale.

Predictor variable (unit) by scale	Expected effect and justification	Source for expectation
Subcontinental (Q1)		
Drought severity (Palmer Drought Severity Index, PDSI)	(+) increased moisture stress on host trees	Raffa et al. (2008), Bentz et al. (2010), Meddens et al. (2012), Williams et al. (2012)
Regional (Q2)		
Elevation (m)	(-) decreased moisture stress on host trees	Maclauchlan (2016), Reich et al. (2016)
Heat Load Index (unitless)	(+) increased moisture stress on host trees	Maclauchlan (2016), Reich et al. (2016)
Subalpine fir abundance (proportion of sub-grid cells with spruce-fir cover)	(-) less stress on subalpine fir trees near core of distribution	Reich et al. (2016)
Stand (Q3)		
Elevation (m)	(-) decreased moisture stress on host trees	Maclauchlan (2016), Reich et al. (2016)
Heat Load Index (unitless)	(+) increased moisture stress on host trees	Bleiker et al. (2005), Maclauchlan (2016), Reich et al. (2016)
Topographic Relative Moisture Index (unitless, scales from 0 to 50)	(-) decreased moisture stress on host trees at more mesic sites	Bleiker et al. (2005), Maclauchlan (2016), Reich et al. (2016)
Stand basal area prior to SFD (m ² /ha)	(+) greater host availability for biotic agents and greater tree stress from competition	McMillin et al. (2003)
Stand stem density prior to SFD (trees/ha)	Same as above	McMillin et al. (2003)
Subalpine fir basal area prior to SFD (m ² /ha)	(+) greater host availability for biotic agents and greater tree stress from competition	McMillin et al. (2003)
Subalpine fir stem density prior to SFD (trees/ha)	Same as above	McMillin et al. (2003)
Proportion of stand basal area prior to SFD that was subalpine fir (prop.)	(+) greater host availability for biotic agents	McMillin et al. (2003)
Proportion of stand density prior to SFD that was subalpine fir (prop.)	(+) greater host availability for biotic agents	McMillin et al. (2003)
Subalpine fir quadratic mean diameter (QMD) prior to SFD (cm)	(+) greater host availability for biotic agents	McMillin et al. (2003), Worrall et al. (2004)
Stand age (age of oldest recorded tree)	(+) greater host availability for biotic agents	Bleiker et al. (2003), Maclauchlan (2016)
Subalpine fir population heterogeneity (coefficient of variation in diameters)	(-) greater stand-structure diversity decreases susceptibility	Raffa et al. (2008)
Tree and tree neighbor (Q4)		
Focal subalpine fir tree size (diameter at 1.37 m height, in cm)	(+) larger trees are more susceptible to biotic agents	Bleiker et al. (2003), Worrall et al. (2004)
Distance to nearest dead subalpine fir tree (0.1 m)	(+) if biotic agents; (-) if abiotic agents	Parish et al. (1999)

Note: The spatial resolution of predictor variables matches the spatial resolution of the response variables in Table 1.

polygons of the presence and intensity of agents of damage or mortality in forested areas. Trained forest health scientists, observing from a fixed-wing aircraft, map polygons with insect and disease damaged trees and then assess the causal agent affecting each host-tree species surveyed. We excluded the southern tip of the Rocky Mountains that extends south of Colorado and

into northern New Mexico as well as the north-western tip of the Rocky Mountains into eastern Washington, as these areas extend into USDA Forest Service regions 3, and 6, respectively, and records for aerial detection survey data prior to the year 2000 were not consistent with the protocols in the Rocky Mountain regions (USDA Forest Service regions 1, 2, and 4). Climatic data

were obtained from the National Oceanic and Atmospheric Administration data portal (<https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp#>), topographic factors were obtained from the 30-m USGS National Elevation Dataset (<https://catalog.data.gov/dataset/usgs-national-elevation-dataset-ned>), and vegetation factors were obtained from the LANDFIRE (Rollins 2009) dataset Environmental Site Potential (ESP; <https://www.landfire.gov/esp.php>).

For the two finest scales (stand and tree/tree neighborhood), data are from thirty-three 0.1-ha field plots located on the eastern slope of the Colorado Front Range in the U.S. Rocky Mountains. In each of three locations spanning 70 km from north to south, plots were located across an elevational gradient (Appendix S1: Table S1). This gradient spanned the lower limit of the spruce-fir forest (lower elevation transition into mid-montane forests dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and ponderosa pine (*Pinus ponderosa*)) to the upper treeline (upper elevation transition into alpine tundra), generally from 2900 to 3450 m, respectively. In order to be included in this study, plots were required to meet the following criteria: at least 40 m²/ha live basal area and 500 live stems/ha prior to recent SFD (approximately the year 2000); at least 15% of the basal area composed of spruce and/or fir (to qualify as spruce-fir subalpine forest); at least 15% of trees composed of subalpine fir (to include stands across a gradient of subalpine fir dominance); and no evidence of recent fire or logging disturbance. Plots were located between 100 and 300 m from the nearest road or trail, and were randomly located in forest stands that met the criteria above; plots were separated by a minimum distance of 500 m.

In each plot, we constructed a 0.1-ha (1018 m) circle plot with four 18-m transect tapes radiating out from the plot center in each of the cardinal directions. Within the entire 0.1-ha plot, all trees taller than 1.37 m and likely to have been standing prior to recent SFD (based on decay class at time of sampling) were recorded with the following data: species, diameter at breast height (dbh at 1.37 m above the ground, to the nearest 0.5 cm), status (live/dead), broken stem (y/n), rooting status (standing or down), and foliar condition if live (percentage of green needles out of

all needles in crown). For all dead trees, we recorded a modified decay class (1, 50–100% red needles; 2, 5–50% red needles; 3, <5% needles, >50% fine branches attached; 4, >50% fine branches fallen; 5, <50% coarse branches detached; 6, >50% coarse branches detached; 7, bark decayed, minimal wood decomposition; 8, decomposing sapwood/heartwood; 9, partially in ground), and any signs of mortality agents. Dead subalpine fir with decay class <8 were assumed to be alive in 2000 at the beginning of the recent SFD episode, whereas dead subalpine fir with decay class ≥8 were assumed to have been dead prior to 2000 and were not included in our quantification of recent SFD severity. This assumption was verified by assessing the decay class in our survey (2016) of a subset of permanently tagged dead subalpine fir trees that were alive in 1994, prior to the recent SFD episode (Smith et al. 2015). Bark beetles were assigned (to the species) if there were exit holes, resin flow, frass or boring dust, and characteristic galleries for western balsam bark beetle (*Dryocoetes confusus*), spruce beetle (*Dendroctonus rufipennis*), mountain pine beetle (*Dendroctonus ponderosae*), Ips sp (*Ips* spp.; Forest Health Protection Rocky Mountain Region 2010). We also noted the presence of Armillaria root rot (*Armillaria* spp.) through the observation of resinosis on the lower tree bole near the root collar and white mycelial mats between bark and sapwood on the lower bole or roots (Forest Health Protection Rocky Mountain Region 2010). Mechanical damage (e.g., from abrasion or neighboring trees falling) was also noted for each tree. We extracted tree cores at a coring height of 1 m from the two largest and presumably oldest Engelmann spruce trees in the plot to estimate stand age. Coordinates (UTM NAD 83) and elevation (m above msl) were recorded for each plot center with a handheld GPS with ±3 m accuracy. Plot slope was measured to the nearest degree with a TruePulse 360 laser rangefinder, and aspect azimuth was measured to the nearest degree with a handheld compass.

On a subset of plots with similar stand density, we also recorded the spatial location of every stem in the plot by measuring the distance (to the nearest 0.1 m) and azimuth (to the nearest degree) from plot center to each tree using a TruePulse 360 laser rangefinder. This was done in 6 plots overall: 3 plots with high-severity SFD

(1 randomly selected plot in each of the three plot locations with SFD mortality >30% of subalpine fir basal area) and 3 plots with low-severity SFD (1 randomly selected plot in each of the three plot locations with SFD mortality <10% of subalpine fir basal area).

Measures of subalpine fir decline

At the two broadest spatial scales (subcontinental and regional), the spatial and temporal extent of SFD was characterized using the ADS dataset. To determine the presence or absence of SFD, we converted the ADS data from its native polygon format into 30-m (0.09-ha) grid cells (aligned with the topographic data, see below) and each grid cell with SFD presence was assigned a 1 and cells with no SFD presence were assigned a 0. Because ADS data are collected at a coarse spatial scale (Johnson and Ross 2008), we then aggregated all 30-m grid cells within an approximate 0.25-km² grid cell (510 × 510 m, or 26 ha) and noted the presence or absence of SFD within each 0.25-km² grid cell. Aggregating ADS data to 0.25-km² grid cells alleviates concern regarding classification accuracy of the native polygon data format (Johnson and Ross 2008) and has been used reliably in many studies (Chapman et al. 2012, Medders et al. 2012, Hart et al. 2015a, b). The aggregation resulted in 981,108 grid cells (255,186 km²) at the subcontinental scale of the U.S. Rocky Mountains and 236,636 grid cells (61,549 km²) at the regional scale of the U.S. Southern Rockies.

At the two finest spatial scales (stand and tree/tree neighborhood), SFD severity was characterized using the field plot dataset. At the stand scale ($n = 33$ plots), the response variable of SFD severity was quantified as the proportion of subalpine fir basal area that died in the recent SFD event—from approximately the year 2000 to time of the 2015/2016 field sampling. This value was computed by dividing the total dead subalpine fir basal area measured in the field (excluding trees assumed to have died prior to 2000, based on decay class) by the total subalpine fir basal area for all trees that were either alive at the time of sampling or recently (since 2000) dead. At the tree and tree-neighborhood scale ($n = 613$ trees total; 308 in high-severity SFD plots, 305 in low-severity SFD plots), the response variable was individual tree

survival or mortality probability for each subalpine fir tree that was assumed to have been alive in 2000 (either alive, or dead since 2000, at time of field data collection).

Measures of potential predictors of subalpine fir decline

At the subcontinental scale (U.S. Rocky Mountains), the potential predictor of SFD extent over time was annual variability in drought severity (Appendix S1: Tables S2, S3). We characterized drought severity with the Palmer Drought Severity Index (PDSI)—a widely used index that incorporates antecedent and current moisture supply and demand to measure cumulative departure in surface water balance (Palmer 1965, Alley 1984). PDSI has been related to tree mortality (Hart et al. 2014a) and is characterized as a standardized value that ranges from approximately −10 to +10 (dry to wet, respectively); values less than −3 characterize severe to extreme drought. To align with the scale of the subcontinental scale, we took the mean PDSI value for the four U.S. Rocky Mountain states (Colorado, Wyoming, Montana, and Idaho; Appendix S1: Table S3).

At the regional scale (Southern U.S. Rocky Mountains), potential predictors of SFD were elevation, heat load index, and host abundance (Appendix S1: Table S2). Elevation (m) was assigned by averaging among the 30 m grid cells that comprise each 0.25-km² grid cell. Heat load index was computed as a unitless index of local microclimate by modifying the potential direct incident solar radiation (MJ cm²/yr) computed from the latitude, aspect, and slope of each 0.25-km² grid cell and shifting the folded aspect axis from 0° and 180° (min and max, respectively) to 45° and 225° (McCune and Keon 2002). Greater values of the heat load index correspond to warmer/drier sites and lesser values correspond to cooler/wetter sites. Host abundance was computed as the proportion of each 0.25-km² grid cell grid cell that was occupied by the class Rocky Mountain spruce-fir forests from the 30-m grid cells in the ESP layer from LANDFIRE (Rollins 2009).

At the stand scale, potential predictors of SFD were three topoclimatic variables and nine stand-structure variables (Table 2; Appendix S1: Table S2). Elevation and heat load index were the same as the regional scale, but measured (or

computed, in the case of heat load index) at the scale of the plot. We also computed an index of relative soil moisture availability for each plot following established methods for a Topographic Relative Moisture Index (TRMI), which incorporates topographic position, slope aspect, slope steepness, and slope configuration (Parker 1982). TRMI can range from a minimum of 0 (warm, dry topographic positions on a very steep southwest facing convex ridgetop) to 50 (cool, wet topographic positions on a shallow-sloped northeast facing concave valley bottom). Actual TRMI values in our plots ranged from 12 to 46 (Appendix S1: Table S2). Potential stand-structure predictor variables at the stand scale included total live tree density, total live basal area, and stand age preceding the recent SFD episode. In addition, we included subalpine fir live tree density, subalpine fir live basal area, the proportion of live stand basal area (and stems) that was subalpine fir, the quadratic mean diameter (QMD) of subalpine fir, and the coefficient of variation (CV) of subalpine fir dbh preceding the recent SFD episode (Table 2; Appendix S1: Table S2). At the tree and tree-neighborhood scale, potential predictors of SFD were the dbh (in cm) for each tree, and the distance to the nearest dead subalpine fir tree (to the nearest 0.1 m).

Data analysis

The nature of the research questions and datasets used to characterize SFD and associated predictor variables varied among the four scales of analyses (Table 1). Therefore, our analyses were specific to each spatial scale.

For Q1 (subcontinental scale), we tested the correlation between the predictor variable (PDSI) and area affected by SFD over the period 1994–2014, using the Pearson correlation coefficient. To account for the 1-year time lag between when mortality agents are affecting a tree and when corresponding tree crown dieback would be observed by ADS personnel, we compared the PDSI of the preceding year to the SFD mapped in a given year (e.g., the PDSI for 1994 was paired with the SFD area in 1995). In addition to the 1-year time lag, we also tested time lags of 0, 2, and 3 yr between annual PDSI and SFD extent (Appendix S1: Table S3).

For Q2 (regional scale), our dataset was the entire wall-to-wall overlap of the response (SFD

presence) and predictor (elevation, heat load index, and spruce-fir forest) variables in each grid cell of the entire study area. That is, our dataset was an entire census of the total area of interest, rather than a sample. For this reason, and as in established methods (Chapman et al. 2012, Hart et al. 2015a), we did not employ a statistical test in Q2; rather, we compared the distribution and median values for each of the predictor variables in areas where SFD was present vs. areas where SFD was absent in the time period 1994–2014.

For Q3 (stand scale), we used a combination of approaches to test the relationship between the response (SFD severity) and predictor (a combination of 12 topoclimate and stand-structure variables, Table 2; Appendix S1: Table S2). We first compared the correlation coefficient for pairwise relationships between SFD severity and each predictor variable (Appendix S1: Fig. S1) and selected the topoclimate variable and the stand-structure variable that had the highest correlation with SFD severity (TRMI and pre-mortality subalpine fir basal area had the top two correlation coefficients with SFD overall). We then built a beta regression model with the *r* package *betareg* (Cribari-Neto and Zeileis 2010) to test the relationship between SFD severity and these top two candidate predictor variables, including potentially significant interaction terms. A nominal 0.01 was added to the response variable of SFD severity for all plots to account for two plots with 0%. Prior to analysis, one plot was excluded from regression models as an outlier because of an anomalously high basal area value—a transcription error that could not be resolved from the original field data—resulting in 32 plots for stand-level analyses. Inclusion or exclusion of this plot did not qualitatively change model results.

For Q4 (tree and tree-neighborhood scale), we built a generalized linear mixed regression model (logistic regression, family binomial) with the *r* package *lme4* (Bates et al. 2015). The model tested the probability of mortality for subalpine fir trees as a function of dbh and distance to the nearest dead subalpine fir tree, with plot included as a random term in the model to account for the hierarchical structure of multiple trees per plot. We were interested in whether the effect of distance to nearest dead subalpine fir

changed with tree size, so we also tested for an interaction term between dbh and distance. We were also interested in seeing if relationships differed between plots with high- or low-severity SFD. Therefore, analyses for Q4 were performed with two models: one model for trees in the three high-severity SFD plots and one model for trees in the three low-severity SFD plots.

RESULTS

Subcontinental scale

At the broadest spatial scale of the U.S. Rocky Mountains, SFD varied over space and time and was strongly associated with temporal variability in broad-scale drought. From 1994 to 2014, 3.9 million ha of forest in the U.S. Rocky Mountains were cumulatively affected by SFD, with mortality prevalence generally greater toward the south (Fig. 1A). The bulk of SFD extent occurred between the years 2000 and 2007 (Fig. 2A); the year with the greatest extent of mortality was 2004, when 375,971 ha were affected. The annual areal extent of SFD was negatively correlated ($r = -0.64$, $P = 0.002$) with PDSI in the previous year in the U.S. Rocky Mountains (Fig. 2A); that is, SFD extent increased in and following years of warm and dry conditions (i.e., years with low PDSI). The relationship with annual SFD and PDSI was similar with 2- and 3-year time lags ($r = -0.60$ and $r = -0.63$, respectively), and weaker with no time lag ($r = -0.45$). The years 2001–2004 were all characterized by regional PDSI values lower than -3.0 (severe to extreme drought) and were immediately followed by the years with the greatest SFD extent (2003–2005).

Regional scale

At the regional scale of the Southern U.S. Rocky Mountains over the years 1994–2014, differences in host-tree abundance and topography between locations of SFD presence and absence were qualitatively minimal compared to the overall range of each variable, but some quantitative differences were observed. Areas of SFD were associated with slightly greater spruce-fir abundance; the proportion of a grid cell occupied by spruce-fir forest was 4% greater in areas of SFD presence (median 90% of grid cell) than SFD absence (median 86% of grid cell) (Fig. 2B). Grid cells with SFD presence were characterized by an

elevation distribution that was similar to the overall distribution of spruce-fir forests, though areas of SFD presence (median 3109 m) were 2% lower elevation than areas of SFD absence (median 3175 m; Fig. 2C). Finally, SFD presence was more associated with cooler and moister topographic positions, as the median heat load was 5% lower in areas of SFD presence (0.83) than areas of SFD absence (0.87; Fig. 2D).

Stand scale

At the stand scale, SFD severity in the field plots ranged from 0 to 62% (median 18%, mean 24%) of subalpine fir basal area killed. SFD severity was most strongly associated with site moisture conditions (TRMI) and host-tree abundance (pre-mortality subalpine fir basal area), with no significant interaction between these factors (Fig. 2E, F; Appendix S1: Table S4). Effect size was slightly greater for TRMI than for host-tree abundance. SFD severity more than doubled from ~15% dead subalpine fir basal area in dry topographic positions (TRMI = 10) to ~40% dead subalpine fir basal area in wet topographic positions (TRMI = 50; Fig. 2E). Comparatively, SFD severity approximately doubled from ~20% dead subalpine fir basal area if pre-mortality subalpine fir basal area was less than 10 m²/ha to ~40% dead subalpine fir basal area if pre-mortality subalpine fir basal area was greater than 60 m²/ha (Fig. 2F).

Tree and tree-neighbor scale

Of the 3,817 subalpine fir trees recorded across all 33 field plots, 891 (24%) were recently dead from SFD (decay class < 8). Among dead trees, 83% had at least one sign of biotic mortality agents; 78% had western balsam bark beetle galleries (of which 49% had no other agent identified), 33% had evidence of *armillaria* sp. fungal hyphae (of which 4% had no other agent identified), and 29% had evidence of both western balsam bark beetle and *armillaria* sp. fungal hyphae. Fourteen percent of dead subalpine fir trees had no evidence of a mortality agent, and 3% of dead subalpine fir trees had evidence of mechanical (e.g., wind or abrasion from neighboring trees) damage leading to death.

At the tree and tree-neighbor scale in high-severity SFD plots (plots with >30% SFD), SFD was strongly associated with tree size and

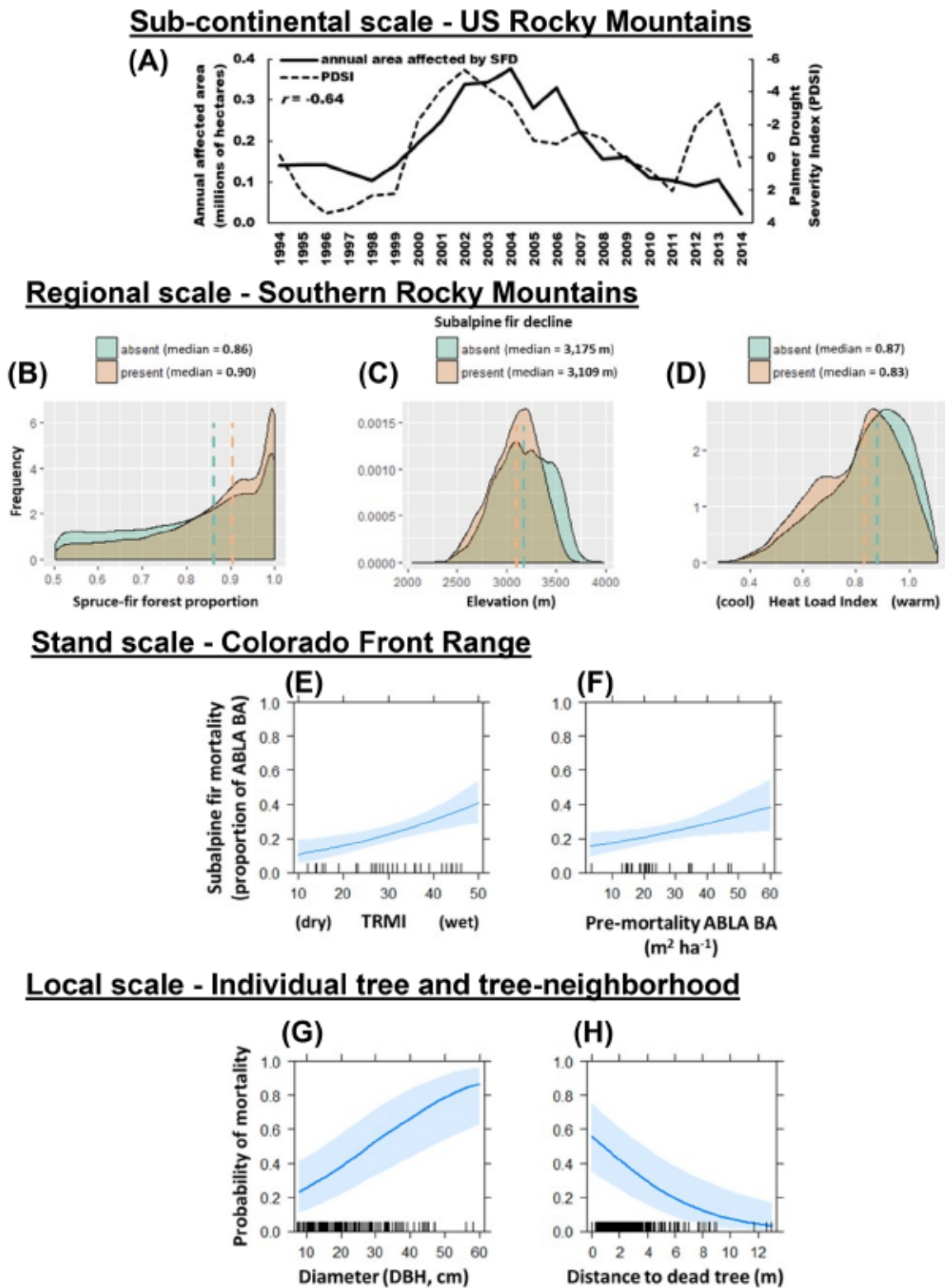


Fig. 2. (A) Correlation between SFD area in each year (solid line) and Palmer Drought Severity Index (PDSI) in

(Fig. 2. Continued)

the preceding year (dashed line) at the subcontinental scale of the U.S. Rocky Mountains. Histograms and medians of areas where SFD is present/absent for three predictor variables: (B) spruce-fir forest proportion; (C) elevation; and (D) heat load index at the regional scale of the Southern Rocky Mountains. Effects plots for beta regression model testing the relationship between SFD severity and the two most important stand-scale predictor variables: (E) Topographic Relative Moisture Index (TRMI) and (F) pre-mortality subalpine fir basal area. Effects plots for generalized linear mixed-effects logistic regression model testing the relationship between mortality of individual subalpine fir trees as a function of (G) dbh and (H) distance to the nearest dead neighboring subalpine fir. For plots E–H, each data point is represented by a short vertical line above the x axis.

distance to nearest dead subalpine fir tree, with no significant interaction between these factors (Fig. 2G,H; Appendix S1: Table S5). The probability of mortality was greater than zero for trees of all sizes; trees at 7.5 cm dbh had a ~ 0.25 probability of mortality, and mortality probability steadily increased with tree size to ~ 0.90 at 60 cm dbh (Fig. 2G). Trees immediately adjacent to dead subalpine fir trees had the highest probability of mortality (approximately 0.55), and the probability of mortality steadily decreased with greater distances from the nearest dead subalpine fir tree; mortality probability was near zero at 10–12 m from the nearest dead neighboring tree (Fig. 2H). For low-severity SFD plots (plots with less than 10% SFD), the positive relationship between tree size and probability of mortality was of marginal significance, and there was no evidence for a relationship between distance to nearest dead tree and probability of mortality or an interaction effect between the factors (Appendix S1: Table S6).

DISCUSSION

At the broadest scale (subcontinental), we found strong support of our hypothesis that temporal variability in drought is important for driving temporal variability in SFD extent. Our findings are similar to those found for other insect outbreaks across North America and Eurasia in that outbreaks track drought in time (Chapman et al. 2012, Williams et al. 2012, Hart et al. 2014a, Seidl et al. 2016, Young et al. 2017). Potential mechanisms for the broad-scale effects of abiotic (climatic controls) are likely a combination of stress effects on trees as well as promoting the population growth for some of the biotic disturbance agents (Raffa et al. 2008). For example,

periods of severe drought can increase moisture stress on trees, particularly shade-tolerant late-seral trees that might be less resistant to drought (Bigler et al. 2007). For subalpine fir, slow growth rates associated with stress have been shown to decrease defensive capacity against attack from WBBB (Bleiker et al. 2005). At the same time, high temperatures that often accompany (or drive) drought can release key constraints on biotic agents such as WBBB. For example, WBBB development and activity are positively related to temperature and are inhibited by low temperatures (Gibson et al. 1997, Negrón and Popp 2009). Collectively, the strong effects of drought on driving temporal variability in SFD extent suggest that if host trees are present, drought is a key inciting factor for SFD.

At regional to stand scales, the conditions associated with spatial variability in SFD extent and severity, respectively, supported complementary insights of those at the subcontinental scale. Whereas temporal variability in SFD extent was driven by broad-scale drought conditions, spatial variability in SFD was more associated with mesic topographic positions and areas of subalpine fir dominance rather than xeric locations where subalpine fir would be assumed to be closer to the edge of physiological tolerance. That is, SFD is driven by hot and dry periods over time, but severity is greatest in areas that are cool, wet, and conducive to biotic interactions associated with tree mortality.

At the regional scale, we did not find support for the hypotheses that SFD presence would be greatest in locations associated with high moisture stress for subalpine fir. For example, SFD was just as likely to be present in locations closer to the core range of subalpine fir than near the edge of the range (Fig. 2B). Individuals near the

edge of a species' range can typically experience greater stress as they are in the zone of physiological tolerance for the geographic niche (Chase and Leibold 2003). However, the marginally greater median proportion of spruce-fir forest in locations with SFD presence than SFD absence suggests that SFD is at least as likely, if not more likely, to occur near the core of the range for subalpine fir rather than at margins. The finding that the median heat load (proxy for spatial variability in moisture stress) was also marginally greater at locations with SFD absence than locations with SFD presence suggests that although subcontinental drought may be driving temporal variability in SFD, locally droughty sites are not more prone to SFD than are locally mesic sites (Lalande et al. 2020).

Our regional-scale spatial analyses did not reveal strong differences between locations of SFD presence and absence within the extent of spruce-fir forests, and minor differences may be within the spatial range of error for our datasets. Future work could address these challenges by applying satellite remote sensing techniques used for mapping spruce beetle outbreak, which have proven promising (Hart and Veblen 2015, Foster et al. 2017). Producing wall-to-wall accurate data on species-level tree occurrence and abundance remains a challenge. Many management jurisdictions (e.g., a single National Forest or a USDA Forest Service Region) have fine-scale (e.g., 30-m pixel) data on vegetation communities. However, methods vary across management jurisdictions based on local objectives, making broad-scale use of such data challenging. Broad-scale data such as the LANDFIRE (Rollins 2009) vegetation data that we use are consistent across management jurisdictions, but are more general to the plant community (e.g., spruce-fir forest) than species-specific. Aerial survey data such as the USDA ADS dataset we used here are useful in that they identify, through expert knowledge, the host tree and probable agent causing tree damage or mortality (Meddens et al. 2012). However, different biotic disturbances have different scales of spatial grain (i.e., the finest resolvable unit of mapping), and aligning the spatial grain of the disturbance with the spatial grain and spatial accuracy of the mapping method remain a challenge (Johnson and Ross 2008, MacLachlan 2016).

At the stand scale, the strong spatial association between SFD severity and mesic locations with greater host-tree abundance has important implications for the role of biotic interactions (insects and pathogens) in tree mortality. All hypotheses that were supported were those associated with locally greater moisture availability and greater biotic disturbance opportunity. The primary factor associated with SFD severity was the plot-scale moisture index (TRMI)—SFD severity more than doubled across the gradient from the driest to the wettest sites. While wetter sites do not indicate greater local drought intensity, they may support biotic agents of disturbance in several ways. First, wetter sites support more and faster growing subalpine fir trees (Andrus et al. 2018, Chai et al. 2019), which may attract and support larger populations of WBBB (Bleiker et al. 2003). At the same time, on an individual level, faster growing subalpine fir trees of a given size are less susceptible to mortality from WBBB (Bleiker et al. 2005). How the trade-off between the positive effects of site moisture on abundant host trees and tree-level vigor influences SFD remains an important question. Second, wetter sites with deeper soils may be more conducive to abundance of *Armillaria* sp. fungi (Worrall et al. 2004), and during warm periods of drought, these wetter sites may be even more conducive to fungal pathogen growth (Lalande et al. 2020). Conversely, on drier sites, soil conditions may be less suitable for buildup of high *Armillaria* sp. populations, and the lower relative abundance of subalpine fir may be less able to support large populations of WBBB. In our plots, depth of the soil organic layer was strongly positively correlated with TRMI ($r = 0.61$, $P < 0.001$; B. Harvey, unpublished data) and may have facilitated fungal growth. Finally, wetter sites are conducive to more rapid subalpine fir growth, which could result in a tree-level trade-off in resource allocation associated with longevity (Bigler and Veblen 2009).

The secondary factor associated with SFD severity at the plot scale was the total basal area of subalpine fir prior to the mortality event, supporting the hypothesis that host abundance for biotic agents is important for spatial variability in SFD. Larger and more abundant subalpine fir trees are important for the most commonly observed biotic mortality agent (WBBB, for

which galleries were observed on 78% of dead trees; Bleiker et al. 2003, McMillin et al. 2003), as well as *Armillaria* sp., which commonly was observed on trees with WBBB galleries (Worrall et al. 2004). This finding is consistent with a stand-scale study of SFD in the southern Rockies (Lalande et al. 2020) and dynamics in other bark beetle outbreaks (Furniss et al. 1979, Amman and Cole 1983, Powers et al. 1999, Simard et al. 2012, Hart et al. 2014b, Seidl et al. 2016), where the availability of large diameter host trees is a key stand-scale predictor of disturbance severity (proportion of trees that die).

Although not selected in the regression model for Q3, the individual relationships between SFD and each of the candidate predictor variables at the stand scale support the finding that mesic locations with greater host abundance are important for local SFD dynamics (Appendix S1: Fig. S1). First, based on relationships between inter-annual climate variation (Q1), SFD could be expected to be greatest in xeric sites. Yet, topoclimatic factors were either unrelated to SFD (e.g., elevation) or related with SFD in ways that demonstrate a positive relationship with cool/wet conditions (e.g., SFD declined with increasing heat load index and SFD increased with increasing TRMI). Second, the increase in SFD with factors that relate to high-productivity sites for subalpine fir (total basal area and proportion basal area composed of subalpine fir) suggests that abundant large subalpine fir trees were most important for SFD. The density of subalpine fir trees was unrelated to SFD at the stand scale, indicating that the total number of trees, regardless of tree size, mattered less. This finding is consistent with the availability of large host trees for biotic disturbance agent being a key requisite for biotic causes of mortality (Furniss et al. 1979, Amman and Cole 1983, Powers et al. 1999, Simard et al. 2012, Hart et al. 2014b, Seidl et al. 2016, Lalande et al. 2020). Finally, factors that correspond to stand-scale structural complexity (e.g., stand age) and heterogeneity (e.g., CV of subalpine fir dbh) were unrelated to SFD, indicating that the amount of large host trees, rather than stand-level heterogeneity, was more important at the stand scale.

Local-scale (tree and tree-neighborhood scale) variability in mortality probability was strongly related to tree size and distance to nearest dead

neighbor, highlighting the importance of biotic factors at fine scales. Between high-severity and low-severity plots that were stem-mapped, there was no difference in stem density and corresponding average distance to nearest neighboring tree for subalpine fir ($P = 0.91$) or all species combined ($P = 0.46$)—indicating that among-tree competition was similar for trees in these plots. As such, if drought stress and competition-related mortality was the primary factor driving mortality, for a given tree, mortality would be expected to be less likely if a neighboring tree died and resources are released. However, we found the opposite, which can be a strong indicator of the key role of contagious biotic agents of mortality such as poorly dispersing insects or fungal pathogens (Larson et al. 2015). In plots with low severity SFD, we found little support for a relationship between tree mortality and tree size and no evidence that distance to nearest dead neighbor was important. Although density did not differ between high- and low-severity SFD plots, subalpine fir QMD was marginally ($P = 0.08$) greater in high-severity than low-severity plots (22.2 and 15.5 cm, respectively), corresponding to a greater number of host trees for biotic agents such as WBBB (Bleiker et al. 2003, McMillin et al. 2003, Lalande et al. 2020). Collectively, this suggests that connectivity among large trees that serve as hosts for biotic disturbance agents was greater in high-severity SFD plots, even though connectivity among host trees irrespective of size was similar. This provides further evidence pointing to the mortality in the recent SFD episode being locally mediated by spatially contagious processes involving WBBB, *Armillaria* sp. fungus, or both, rather than from abiotic-driven stress alone (Lalande et al. 2020).

Collectively, our finding that broad-scale temporal variability in SFD corresponds to periods of drought and that spatial variation in SFD extent and severity corresponds to mesic locations with greater host-tree abundance suggest implications for mechanisms that could be tested in future research. Xeric sites, while more exposed to the direct effects of drought, may be serving as topographic refugia from SFD as the relative scarcity of subalpine fir could drive less exposure to biotic agents of mortality. This mechanism has been suggested in other conifer-

dominated systems experiencing recent drought-related mortality and warrants further exploration (McDowell et al. 2019). Additionally, our data could mean that locally moist and cool sites, which may be better for rapid tree growth, could be also areas of high mortality and rapid population turnover (Bigler and Veblen 2009, Redmond and Kelsey 2018). Trees in drier sites could potentially allocate more carbon to root development than trees in moister sites and therefore be more buffered from the effects of severe drought periods such as those that occurred from 2001 to 2004 in the Rocky Mountains. As such, whether subalpine fir is actually experiencing greater drought stress in xeric sites than mesic sites is unknown. Radial growth of subalpine fir may be more sensitive to climatic fluctuations than other co-occurring species in mesic sites, even when responses to climate are similar in xeric sites (Vilalba et al. 1994). This sensitivity may lead to greater susceptibility to drought-driven mortality for subalpine fir than for co-occurring tree species (Bigler et al. 2007). To address these uncertainties, future studies could measure tree ecophysiological responses across a moisture gradient and/or populations of biotic agents of mortality across a host-abundance gradient. Research at the stand and tree scale on the mechanisms of SFD remains a research priority.

CONCLUSIONS

By integrating data across scales spanning several orders of magnitude, we uncover key insights about the factors associated with SFD—a widespread, but poorly understood forest disturbance. Specifically, broad (e.g., subcontinental) scale temporal patterns in SFD extent were associated with temporal patterns in drought. However, regional-, stand-, and local-scale spatial patterns of SFD extent, severity, and individual tree mortality were associated with mesic topographic positions, greater host abundance, and connectivity for biotic agents of mortality. This positive temporal association with drought at broad scales and negative spatial association with xeric sites at local scales highlights the role of scale in understanding the mechanisms driving ecological disturbance. That is, inferences drawn from broad-scale trends about the importance of drought over

time could be misleading if applied to spatial variability at local scales, where SFD severity was greatest on mesic sites and where the host tree was abundant. Conversely, trees in xeric sites were the least susceptible to SFD and suggest that life-history trade-offs or refuge from biotic agents of mortality may be important for persistence in a warming climate.

ACKNOWLEDGMENTS

We thank Garth Omelas, Ashley Hoffman, Carah Bordner, Shala Wallace, Rachel Chai, and C. J. Cornell for help with fieldwork. The Arapaho-Roosevelt National Forest, the Niwot Ridge LTER station, and the University of Colorado Mountain Research Station provided logistical support and site access. Funding for this research was provided by the David H. Smith Conservation Research Fellowship Program awarded to B.J. Harvey. We also thank the NSF LTER Research Experiences for Undergraduates (REU) Program, the NSF Research Experience for Community College Students (RECCS) program administered through the University of Colorado Cooperative Institute for Research in Environmental Sciences program, and the NSF UNAVCO summer internship program for supporting paid field interns. We thank two anonymous reviewers and D. Breshears for their helpful comments in improving an earlier version of this manuscript. The authors declare no conflict of interest.

LITERATURE CITED

- Allen, C. D., D. D. Breshears, and N. G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:art129.
- Alley, W. M. 1984. The Palmer drought severity index: limitations and assumptions. *Journal of Climate and Applied Meteorology* 23:1100–1109.
- Amman, G. D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests: Part II. Population dynamics. General Technical Report INT-145. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Anderegg, W. R. L., et al. 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *New Phytologist* 208:674–683.
- Andrus, R. A., B. J. Harvey, R. K. Chai, and T. T. Veblen. 2018. Different vital rates of Engelmann spruce and subalpine fir explain discordance in understory and overstory dominance. *Canadian Journal of Forest Research* 48:1554–1562.

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602–613.
- Bigler, C., D. G. Gavin, C. Gunning, and T. T. Veblen. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos* 116:1983–1994.
- Bigler, C., and T. T. Veblen. 2009. Increased early growth rates decrease longevity of conifers in subalpine forests. *Oikos* 118:1130–1138.
- Bleiker, K. P., B. S. Lindgren, and L. E. MacLauchlan. 2003. Characteristics of subalpine fir susceptible to attack by western balsam bark beetle (Coleoptera: Scolytidae). *Canadian Journal of Forest Research* 33:1538–1543.
- Bleiker, K. P., B. Staffan Lindgren, and L. E. MacLauchlan. 2005. Resistance of fast- and slow-growing subalpine fir to pheromone-induced attack by western balsam bark beetle (Coleoptera: Scolytidae). *Agricultural and Forest Entomology* 7:237–244.
- Chai, R. K., R. A. Andrus, K. Rodman, B. J. Harvey, and T. T. Veblen. 2019. Stand dynamics and topographic setting influence changes in live tree biomass over a 34-year permanent plot record in a subalpine forest in the Colorado Front Range. *Canadian Journal of Forest Research* 49:1256–1264.
- Chapman, T. B., T. T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. *Ecology* 93:2175–2185.
- Chase, J. M., and M. A. Leibold. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, Illinois, USA.
- Cribari-Neto, F., and A. Zeileis. 2010. Beta regression in R. *Journal of Statistical Software* 34:1–24.
- Diskin, M., M. E. Rocca, K. N. Nelson, C. F. Aoki, and W. H. Romme. 2011. Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research* 41:782–792.
- Falk, D. A., C. Miller, D. McKenzie, and A. E. Black. 2007. Cross-scale analysis of fire regimes. *Ecosystems* 10:809–823.
- Forest Health Protection Rocky Mountain Region. 2010. Field guide to diseases & insects of the Rocky Mountain Region. Page 336. General Technical Report GTR-241, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Foster, A. C., J. A. Walter, H. H. Shugart, J. Sibold, and J. Negrón. 2017. Spectral evidence of early-stage spruce beetle infestation in Engelmann spruce. *Forest Ecology and Management* 384:347–357.
- Furniss, M. M., M. D. McGregor, M. W. Foiles, and A. D. Partridge. 1979. Chronology and characteristics of a Douglas-fir beetle outbreak in northern Idaho. General Technical Report INT-59. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Gibson, K. E., S. Kegley, and R. D. Oakes. 1997. Western balsam bark beetle activity and flight periodicity in the Northern Region. Page 5. General Technical Report CFFH-97-3. USDA Forest Service Cooperative for Forestry and Forest Health, Missoula, Montana, USA.
- Hart, S. J., T. Schoennagel, T. T. Veblen, and T. B. Chapman. 2015a. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proceedings of the National Academy of Sciences of the United States of America* 112:4375–4380.
- Hart, S. J., T. T. Veblen, N. Mietkiewicz, and D. Kulakowski. 2015b. Negative feedbacks on bark beetle outbreaks: Widespread and severe spruce beetle infestation restricts subsequent infestation. *PLOS ONE* 10:e0127975.
- Hart, S. J., and T. T. Veblen. 2015. Detection of spruce beetle-induced tree mortality using high- and medium-resolution remotely sensed imagery. *Remote Sensing of Environment* 168:134–145.
- Hart, S. J., T. T. Veblen, K. S. Eisenhart, D. Jarvis, and D. Kulakowski. 2014a. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology* 95:930–939.
- Hart, S. J., T. T. Veblen, and D. Kulakowski. 2014b. Do tree and stand-level attributes determine susceptibility of spruce-fir forests to spruce beetle outbreaks in the early 21st century? *Forest Ecology and Management* 318:44–53.
- Johnson, E. W., and J. Ross. 2008. Quantifying error in aerial survey data. *Australian Forestry* 71:216–222.
- Kautz, M., A. J. H. Meddens, R. J. Hall, and A. Arneeth. 2017. Biotic disturbances in Northern Hemisphere forests - a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. *Global Ecology and Biogeography* 26:533–552.
- Lalande, B. M., K. Hughes, W. R. Jacobi, W. T. Tinkham, R. Reich, and J. E. Stewart. 2020. Subalpine fir mortality in Colorado is associated with stand density, warming climates and interactions among

- fungus diseases and the western balsam bark beetle. *Forest Ecology and Management* 466:118133.
- Larson, A. J., J. A. Lutz, D. C. Donato, J. A. Freund, M. E. Swanson, J. HilleRisLambers, D. G. Sprugel, and J. F. Franklin. 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology* 96:2855–2861.
- Lausch, A., M. Heurich, and L. Fahse. 2013. Spatiotemporal infestation patterns of *Ips typographus* (L.) in the Bavarian Forest National Park, Germany. *Ecological Indicators* 31:73–81.
- Lloret, F., A. Escudero, J. M. Iriondo, J. Martínez-Vilalta, and F. Valladares. 2012. Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology* 18:797–805.
- MacLachlan, L. 2016. Quantification of *Dryocoetes confusus*-caused mortality in subalpine fir forests of southern British Columbia. *Forest Ecology and Management* 359:210–220.
- McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13:603–606.
- McDowell, N. G., et al. 2019. Mechanisms of a coniferous woodland persistence under drought and heat. *Environmental Research Letters* 14:045014.
- McMillin, J. D., K. K. Allen, D. F. Long, and J. F. Negrón. 2003. Effects of western balsam Bark Beetle on Spruce-Fir forests of north-central Wyoming. *Western Journal of Applied Forestry* 18:8.
- Meddens, A. J., J. A. Hicke, and C. A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications* 22:1876–1891.
- Meentemeyer, R. K., S. E. Haas, and T. Václavík. 2012. Landscape epidemiology of emerging infectious diseases in natural and human-altered ecosystems. *Annual Review of Phytopathology* 50:379–402.
- Negrón, J. F., and J. B. Popp. 2009. The flight periodicity, attack patterns, and life history of *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), the western balsam bark beetle, in north central Colorado, Western North. *American Naturalist* 69:447–458.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* 77:118–125.
- Palmer, W. C. 1965. Meteorological drought. Research Paper No. 45. US Weather Bureau, Office of Climatology, Washington, D.C., USA.
- Parish, R., J. A. Antos, and M.-J. Fortin. 1999. Stand development in an old-growth subalpine forest in southern interior British Columbia. *Canadian Journal of Forest Research* 29:1347–1356.
- Park Williams, A., et al. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change* 3:292–297.
- Parker, A. J. 1982. The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Physical Geography* 3:160–168.
- Pataki, D. E., R. Oren, and W. K. Smith. 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology* 81:2557–2566.
- Peters, D. P. C., A. E. Lugo, F. S. Chapin, S. T. A. Pickett, M. Duniway, A. V. Rocha, F. J. Swanson, C. Laney, and J. Jones. 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2:art81.
- Peters, D. P. C., R. A. Pielke, B. T. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *Proceedings of the National Academy of Sciences of the United States of America* 101:15130–15135.
- Powers, J. S., P. Sollins, M. E. Harmon, and J. A. Jones. 1999. Plant-pest interactions in time and space: A Douglas-fir bark beetle outbreak as a case study. *Landscape Ecology* 14:105–120.
- Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience* 58:501–517.
- Redmond, M. D., and K. C. Kelsey. 2018. Topography and overstory mortality interact to control tree regeneration in spruce-fir forests of the southern Rocky Mountains. *Forest Ecology and Management* 427:106–113.
- Reich, R. M., J. E. Lundquist, and K. Hughes. 2016. Host-environment mismatches associated with subalpine fir decline in Colorado. *Journal of Forestry Research* 27:1177–1189.
- Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire* 18:235.
- Seidl, R., et al. 2017. Forest disturbances under climate change. *Nature Climate Change* 7:395–402.
- Seidl, R., J. Müller, T. Hothorn, C. Bässler, M. Heurich, and M. Kautz. 2016. Small beetle, large-scale drivers: how regional and landscape factors affect outbreaks of the European spruce bark beetle. *Journal of Applied Ecology* 53:530–540.
- Senf, C., E. M. Campbell, D. Pflugmacher, M. A. Wulder, and P. Hostert. 2017. A multi-scale analysis of western spruce budworm outbreak dynamics. *Landscape Ecology* 32:501–514.

- Simard, M., E. N. Powell, K. F. Raffa, and M. G. Turner. 2012. What explains landscape patterns of tree mortality caused by bark beetle outbreaks in Greater Yellowstone?: Landscape patterns of bark beetle outbreaks. *Global Ecology and Biogeography* 21:556–567.
- Smith, J. M., J. Paritsis, T. T. Veblen, and T. B. Chapman. 2015. Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. *Forest Ecology and Management* 341:8–17.
- Veblen, T. T. 1986. Age and Size Structure of Subalpine Forests in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* 113:225.
- Veblen, T. T., K. S. Hadley, M. S. Reid, and A. J. Rebertus. 1991. The response of subalpine forests to spruce beetle outbreak in Colorado. *Ecology* 72:213–231.
- Villalba, R., T. T. Veblen, and J. Ogden. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. *Ecology* 75:1450–1462.
- Worrall, J. J., K. F. Sullivan, T. C. Harrington, and J. P. Steimel. 2004. Incidence, host relations and population structure of *Armillaria ostoyae* in Colorado campgrounds. *Forest Ecology and Management* 192:191–206.
- Young, D. J. N., J. T. Stevens, J. M. Earles, J. Moore, A. Ellis, A. L. Jirka, and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20:78–86.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3318/full>