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# Summer and winter drought drive the initiation and spread of spruce beetle outbreak

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*Abstract.* This study used Landsat-based detection of spruce beetle (*Dendroctonus rufipennis*) outbreak over the years 2000–2014 across the Southern Rocky Mountain Ecoregion to examine the spatiotemporal patterns of outbreak and assess the influence of temperature, drought, forest characteristics, and previous spruce beetle activity on outbreak development. During the 1999–2013 period, time series of spruce beetle activity were highly spatially correlated ($r > 0.5$) at distances <5 km, but remained weakly correlated ($r = 0.08$) at distances >400 km. Furthermore, cluster analysis on time series of outbreak activity revealed the outbreak developed at multiple incipient locations and spread to unaffected forest, highlighting the importance of both local-scale dispersal and regional-scale drivers in synchronizing spruce beetle outbreak. Spatial overlay analysis and Random Forest modeling of outbreak development show that outbreaks initiate in areas characterized by summer, winter, and multiyear drought and that outbreak spread is strongly linked to the proximity and extent of nearby outbreak, but remains associated with drought. Notably, we find that spruce beetle outbreak is associated with low peak snow water equivalent, not just summer drought. As such, future alterations to both winter and summer precipitation regimes are likely to drive important changes in subalpine forests.

*Key words: aerial detection survey data; bark beetle;* Dendroctonus; *drought; Engelmann spruce; Landsat; snow water equivalent; spatial synchrony.*

## Introduction

Recent warm temperatures and drought have been linked to increased tree mortality around the world (Allen et al. 2010), with cascading consequences for biogeochemical cycling, hydrology, forest structure and composition, and wildlife habitat (Vose et al. 2016). Drought may directly lead to tree death through hydraulic failure and/or carbon starvation (McDowell et al. 2011, Sala et al. 2012) and/or indirectly by increasing the frequency, severity, or extent of drought-sensitive disturbances (Vose et al. 2016). Outbreaks of bark beetles (Curculionidae: Scolytinae) are important drought-sensitive disturbances affecting North American forests, where synchronous outbreaks have caused extensive tree mortality across 6.6 Mha 1997–2012 (Hicke et al. 2016). Given that future changes in climate are expected to alter patterns of drought across the much of the western United States (Swain and Hayhoe 2015), it is critical to understand how drought affects the initiation and spread of bark beetle outbreaks.

In the Southern Rocky Mountain Ecoregion (SRME; U.S. EPA 2011), outbreaks of spruce beetles (*Dendroctonus rufipennis*) are key disturbances in Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests. The spruce beetle inhabits the inner bark and feeds on the tree's phloem. Extensive colonization and reproduction typically leads to tree death, however at low population levels, spruce beetles typically infest weakened trees (Schmid and Frye 1977, Jenkins et al. 2014). As beetle populations rise, pheromone-mediated cooperative attack allows beetles to infest better defended trees (Wallin and Raffa 2004).

In the Southern Rockies spruce beetles typically have a 2-yr life cycle, although favorable weather conditions may allow beetles to complete a generation in one year (univoltine) (Knight 1961, Hansen et al. 2001). Adults typically emerge from early June through late July (Jorgensen 2003) and attack new trees, where females deposit their eggs. After eggs are laid, they begin to develop, which typically pauses in October. Prepupal larvae resume development the following summer, when they pupate and hatch. New adults overwinter in the tree and emerge the following summer (Schmid and Frye 1977). Warm summer temperatures increase the odds that prepupal larvae will pupate and develop into adults prior to winter, thereby completing their life cycle in only one year (Knight 1961, Hansen et al. 2001).

Eruption to outbreak stages is complex but requires abundant suitable hosts, often determined by disturbance and/or land use history (Veblen et al. 1994). Given a susceptible landscape, outbreaks may be incited by events

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that accelerate beetle population growth rates, notably warm summer temperatures, which promote a univoltine lifecycle (Knight 1961, Hansen et al. 2001), and above-average winter temperatures, which increase the survival rates of overwintering beetles (Miller and Werner 1987). Outbreaks may also be incited by drought-induced changes in tree defense, including resin flow, which provides a physical barrier, and the production of induced and constituent chemicals (primarily terpenes), which may repel or kill beetles (Christiansen et al. 1987). At low levels of drought, trees are expected to allocate more resources to defense and less to growth. Thus at low to moderate water stress when growth is constrained more than photosynthesis, trees might be less susceptible to infestation (Herms and Mattson 1992). However, intense drought reduces resin flow and carbon assimilation (McDowell et al. 2011, Sala et al. 2012) and limits the production of defense compounds. Thus severe drought may decrease tree resistance to infestation (Herms and Mattson 1992). While severely stressed trees may be more susceptible to infestation, excessively low photosynthate production might not provide adequate nutrition to support larval development (Raffa and Berryman 1983).

Analyses of tree-ring records show that periods of broad-scale spruce beetle outbreak occur synchronously through time, indicative of a regional driver (Sherriff et al. 2011, Hart et al. 2014*a*). Indeed, periods of outbreak often co-occur with above-average winter and summer temperatures and drought (Berg et al. 2006, Hebertson and Jenkins 2008, Sherriff et al. 2011, DeRose and Long 2012, Hart et al. 2014*a*). Yet not all periods of favorable climate are associated with outbreak (Hart et al. 2014*a*) and not all spruce become infested during periods of outbreak (Veblen et al. 1994). Instead, outbreaks develop when key thresholds are surpassed, prior constraints fail to limit infestation, and positive feedbacks maintain high beetle populations (Raffa et al. 2008). Although the mechanisms and feedbacks that lead to spruce beetle infestation at the tree and stand scale have been the topic of much research (for a review, see Jenkins et al. 2014), the mechanisms of outbreak initiation and spread across heterogeneous landscapes are less clear.

Analysis of spatial patterns of bark beetle populations can provide insight into the drivers of outbreak development (Aukema et al. 2006, Chapman et al. 2012). Across broad areas, synchronous changes in population size are hypothesized to occur due to dispersal, species interactions (e.g., predation), and synchronous changes in a density-independent factor (e.g., weather), a phenomenon known as the Moran effect (Moran 1953). In the case of the spruce beetle, the degree to which populations are synchronized due to dispersal vs. the development of endemic local populations is unclear. If spatially synchronous outbreaks are driven entirely by dispersal, then we would expect outbreak to spread from a single epicenter. Conversely, if spatially synchronous changes in exogenous factors drive the occurrence of synchronous outbreaks, then there should be multiple origin points. A better understanding of the drivers of spruce beetle outbreak is critical to predicting future dynamics of subalpine forests.

Here we use Landsat data to map spruce beetle outbreak over the 1999–2013 period in the SRME and seek to quantify the relative contributions of exogenous (e.g., drought, temperature) and endogenous factors (e.g., spruce beetle dispersal, host tree abundance) in driving spatiotemporal patterns. Specifically, we seek to answer the following three questions: (1) Did the current spruce beetle outbreak originate at multiple locations or diffuse from a single location? (2) How does the temporal synchrony of spruce beetle activity, drought, and temperature change with distance? (3) How is outbreak initiation and spread associated with timing and severity of drought, temperature conditions favorable for outbreak, forest characteristics, and beetle dispersal?

## Methods

### *Study area*

The study area is the spruce–fir zone of the SRME, which extends from northern New Mexico to southern Wyoming (Fig. 1). The area of spruce–fir forest was defined by combining four spatial data sets of vegetation cover-type (Appendix S1: Table S1). We combined data sets by listing the presence of spruce–fir only when two or more data sets were in agreement (Preisler et al. 2012). Within the SRME, spruce–fir forest is found at upper-elevation sites (~2,000–4,000 m), which are characterized by cold, wet winters (mean January temperature of −7.6°C and mean total December–March precipitation of 233 mm; 1981–2010; PRISM Climate Group 2013) and warm, dry summers (mean July temperature 13.1°C and mean total June–August precipitation 172 mm; 1981–2010; PRISM Climate Group 2013). The dominant tree species include Engelmann spruce and subalpine fir, and to a lesser extent lodgepole pine (*Pinus contorta* var. *latifolia*), limber pine (*Pinus flexilis*), and trembling aspen (*Populus tremulodies*).

### *Data*

*Spruce beetle outbreak.*—We analyzed spatiotemporal patterns of spruce beetle outbreak derived from Landsat imagery for the 2000–2014 period following methods outlined in Hart and Veblen (2015). Briefly, the presence of gray-stage outbreak within spruce–fir forests was mapped using multi-temporal trends in Landsat-based vegetation indices sensitive to tree mortality. The resulting maps represent accurate fine-grain (30 × 30 m) records of the spatiotemporal development of tree mortality due to spruce beetle outbreak (overall accuracy and user's accuracy for gray stands inferred to be affected by spruce beetles 90% and 88%, respectively; Hart and Veblen 2015). To account for the ~1-yr lag between initial infestation and needle drop when stands exhibit different spectral signatures (Jenkins et al. 2014),

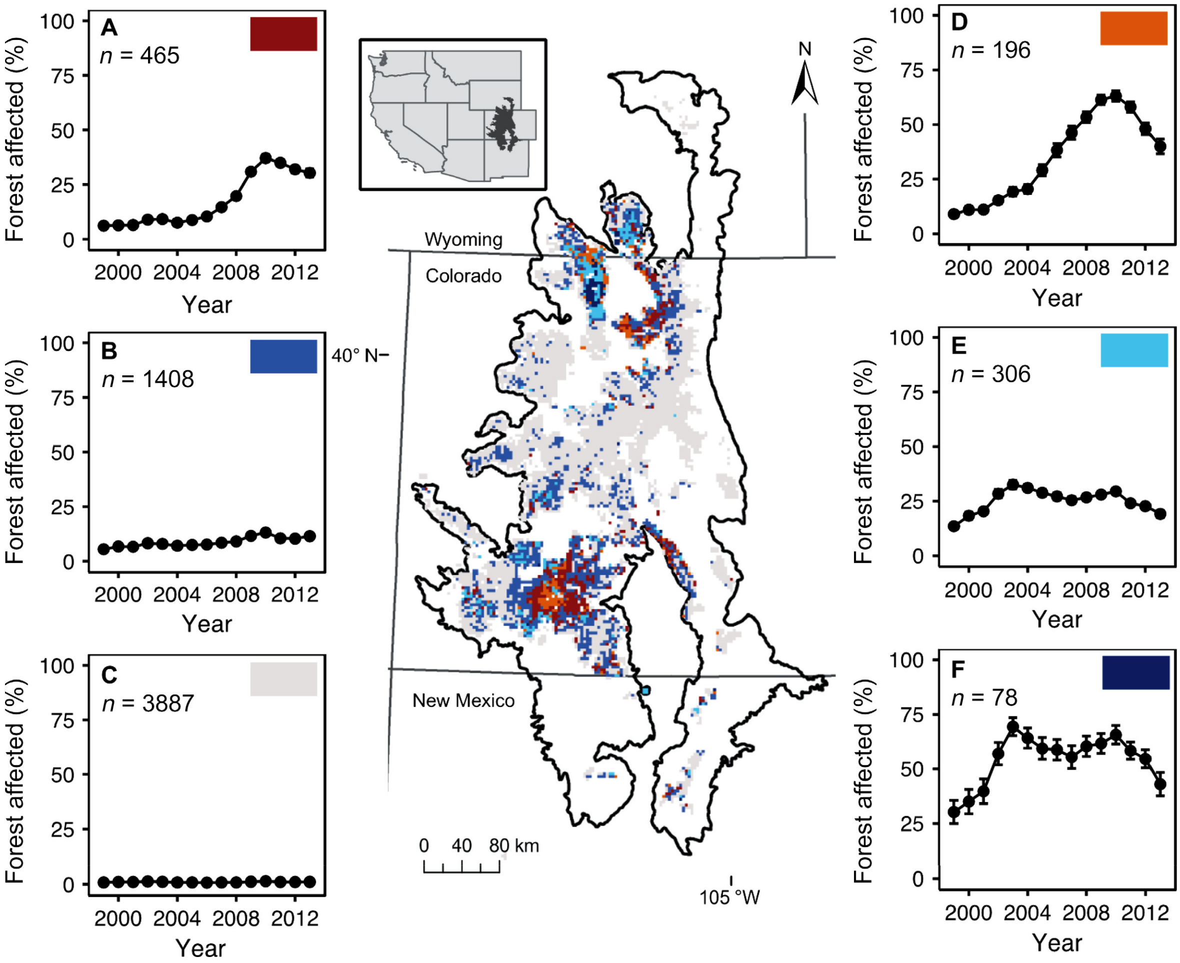

FIG. 1. *K*-means cluster analysis of time series (1999–2013) of spruce beetle activity in spruce–fir forests across the Southern Rocky Mountain Ecoregion (SRME; $k$ = 6 clusters). The inset displays the location of the SRME relative to the contiguous western United States. Time series patterns (means ± SE) of outbreak activity for clusters A–F are graphically presented in panels A–F. Note that the color in the corner of each time series plot serves as a legend for the map. [Color figure can be viewed at wileyonlinelibrary.com]

we followed the suggestion of Meddens and Hicke (2012) and lagged annual maps of spruce beetle outbreak by one year (i.e., from 2000–2014 to 1999–2013).

While spruce beetle outbreak is the predominant disturbance across the SRME spruce–fir zone, differentiating among disturbances using vegetation indices alone can be difficult. Aerial Detection Survey (ADS; USFS 2015) data can be used to improve Landsat-based maps of bark beetle outbreak (Meigs et al. 2011), however, ADS data depicts coarse-scale outbreak (>500 m) and not all areas are surveyed annually (Johnson and Wittwer 2008). Given the limitations of using ADS data in spatiotemporal analyses, we created a map of cumulative ADS-detected spruce beetle outbreak (1997–2014) and buffered it by 1 km to represent areas of possible outbreak. Pixels of spruce beetle activity in the Landsat-based grids that overlaid areas of ADS-based possible outbreak were referred to as affected; ones that did not were referred to as unaffected. We removed recently burned areas, areas harvested 0–10 yr before outbreak, and areas of blowdown (Appendix S1: Table S1). Finally, to reduce the effects of fine-scale spruce beetle dispersal, which typically occurs within 300 m (Werner and Holsten 1997), we aggregated 30 × 30 m grids of the presence/absence of outbreak to a 300 × 300 m grid (Appendix S1: Table S1).

*Temperature and drought variables.*—To understand the potential effects of temperature and drought on spruce beetle activity, we obtained 4 × 4 km grids of monthly temperature and precipitation from PRISM (data set AN81d; PRISM Climate Group 2013) (Appendix S1: Table S1), which have been widely used in ecological studies across the mountainous U.S. West (e.g., Chapman et al. 2012). Data were then statistically downscaled using moderate-scale (800 × 800 m) 1981–2010 climate normals from PRISM. Given the sensitivity of spruce beetles to summer and winter temperatures (Miller and Werner 1987, Hansen et al. 2001), we acquired the average maximum daily temperatures for August (Aug TMAX) and average daily minimum temperatures for December (Dec TMIN) (Appendix S1: Table S1). We also included three indices of drought to represent the sensitivity of host trees to water stress (DeRose and Long 2012, Hart et al. 2014*a*). We used PRISM data to calculate the Standardized Evapotranspiration Precipitation Index (SPEI), which accounts for both precipitation and potential evapotranspiration (Vicente-Serrano et al. 2010). We calculated SPEI for the June–July period (Jun–Jul SPEI) and a 5-yr period, which spanned September to the October five years prior (i.e., five water years; 5-yr SPEI). Finally, because spruce may rely heavily upon snowmelt water (Hu et al. 2010, Winchell et al. 2016), we included a spatial estimate of peak annual snow water equivalent (peak SWE), which typically occurs between late March and late May in the SRME (Winchell et al. 2016). SWE data were derived from a fusion of the National Resource Conservation Service Snow Telemetry (SNOTEL) SWE observations, topographic variables and remotely sensed data (Schneider and Molotch 2016). To ensure a temporal match between temperature and drought variables and the spruce beetle cycle, we assumed a univoltine lifecycle, which increases potential for outbreak (Hansen and Bentz 2003, Berg et al. 2006). Thus peak SWE was calculated for spring prior to attack, Aug TMAX, Jun–Jul SPEI, 5-yr SPEI were calculated for the summer of attack, and Dec TMIN was calculated for the winter following attack.

*Forest characteristics.*—As a proxy for stand density, which increases the susceptibility of spruce–fir stands to outbreak (Schmid and Frye 1977), we acquired Landsat-based maps of percent tree cover in 2000 (Sexton et al. 2013). For each 300 × 300 m pixel, we calculated the mean percent tree cover. Given that spruce beetles outbreak is more common in stands with large diameter trees (>20 cm diameter at breast height (DBH); Schmid and Frye 1977, Jenkins et al. 2014), we acquired maps of the dominant tree size (USFS 2003). We then calculated the proportion of each 300 × 300 m pixel dominated by large trees (>22 cm in DBH; dominance of large trees). Finally, we calculated the area of spruce–fir forest within each pixel (area of spruce–fir). While the relative dominance of spruce may also influence stand-scale infestation (Schmid and Frye 1977), geospatial data of this kind are not available and thus it is not accounted for in our model.

*Spruce beetle dispersal pressure.*—As a proxy for spruce beetle dispersal, we used the extent and proximity of spruce beetle outbreak at the previous time step. Mark and recapture studies suggest that most spruce beetle dispersal occurs within 300 m, but that long distance dispersal may occur at distances up to 1 km (Werner and Holsten 1997). To this end we created a proxy for spruce beetle dispersal pressure (dispersal pressure), defined as the number of spruce beetle affected cells in a ~1 km neighborhood at the previous time step. Following methods for quantifying mountain pine beetle dispersal pressure outlined by Preisler et al. (2012), we applied an inverse sigmoidal curve with weights of 1.0, 0.5, and 0.1 in the cells at 300, 600 m and 900 m distant, respectively.

### *Determining the spatiotemporal development of spruce beetle outbreak*

To determine if the current outbreak originated from multiple points or erupted from a central location, we used a cluster analysis on time series of spruce beetle outbreak (Aukema et al. 2006). Because cluster analysis works best on continuous variables, we created an index of outbreak activity, defined as the area of affected forest divided by the area of spruce–fir within 3 × 3 km grids. Clusters were then constructed from the 15-yr time series of outbreak activity using *K*-means cluster analysis (Hartigan and Wong 1979). The optimum number of clusters was selected visually using a sum of squared error scree plot (Hothorn and Everitt 2009) (Appendix S2). Clusters were then mapped onto the study area in a GIS and the spatial arrangement and associated time series were visually interpreted.

### *Quantifying the spatial dependence of temporal synchrony of spruce beetle outbreak, temperature, and drought*

We quantified the spatial scale at which spruce beetle outbreak occurs synchronously using a smoothed nonparametric covariance function, which estimates the spatial dependence of time series covariance (Bjørnstad and Falck 2001). Time series of spruce beetle affected forest were used to calculate cross correlations using the midpoint of each 300 × 300 m grid cell as the spatial reference. Confidence intervals around the covariance function were calculated using a bootstrap resampling approach with 1000 replications. We then calculated smoothed nonparametric covariance functions for annual weather variables potentially associated with outbreak (Aug TMAX, Dec TMIN, Jun–Jul SPEI, 5-yr SPEI, and peak SWE).

### *Determining the drivers of outbreak spread and initiation*

To determine the endogenous and exogenous drivers of initiation and spread of spruce beetle outbreak, for each pixel, we determined the initial year of outbreak and examined biophysical variables during this initial year of attack. Because the development of outbreak is expected to be strongly associated with the proximity of neighboring populations of spruce beetles and this may mask the effects of biophysical drivers (Raffa et al. 2008), we divided affected pixels into *outbreak initiation*, defined as pixels where dispersal pressure equals zero, and *outbreak spread*, defined as pixels where dispersal pressure was greater then zero. We then used two approaches to assess the association of outbreak initiation and spread with spatial variability in drought, temperature, forest characteristics, and dispersal pressure.

First, we used a spatial overlay approach, where grids of spruce beetle affected forest were overlaid with grids of biophysical variables. Continuous biophysical variables were binned into five equal-interval classes. Then we tabulated the observed area of outbreak initiation and spread in each class of the independent variable. Observed areas were compared with an *expected* area, which is proportional to the total area in each class of the independent variable (O'Sullivan and Unwin 2010). Given that our spatial data sets exhibit classification error, we conservatively assumed that only differences >10% were meaningful.

Second, we used a Random Forest (RF) approach to understand the drivers of outbreak initiation and spread. RF provides high classification accuracy and has been shown to be useful for modeling complex interactions among ecological variables (Cutler et al. 2007). We constructed two RF models: (1) an outbreak initiation model, which uses abiotic and biotic variables to identify the drivers of presence/absence of outbreak occurrence when dispersal pressure was equal to zero and (2) an outbreak spread model, which uses abiotic and biotic variables to identify the drivers of presence/absence of outbreak occurrence when dispersal pressure was greater than zero. Both models were constructed from a random sample of pixels, which were stratified by outbreak stage (375 affected and 375 unaffected pixels). Sample size was selected to maximize the number of outbreak initiation pixels. Model fit was evaluated using the internal out-of-bag coefficient of determination, which is constructed from data withheld from model construction. To evaluate the variables most important for predicting spruce beetle initiation and spread, we calculated the mean decrease in accuracy statistic, a measure of each predictor's contribution to model fit (Breiman 2001). While variable importance scores may be sensitive to multicollinearity, none of our predictor variables were strongly correlated (defined as $r > 0.6$) (Appendix S3). To visualize the main effect of the most important predictor variables, we constructed partial dependence plots (Friedman 2001).

## RESULTS

### *Did the current spruce beetle outbreak originate at multiple locations or diffuse from a single location?*

Across the SRME, spruce beetle outbreak affected approximately 29% of the spruce-fir zone over the period from 2000 to 2014. Cluster analysis revealed six unique cluster types for spruce beetle activity were identified (Fig. 1; Appendix S2: Fig. S1). The most common cluster type, Cluster C, represents unaffected pixels (Fig. 1C). Clusters E and F, which are predominantly located in the northern portion of the SRME, show the earliest signs of spruce beetle activity with increasing activity from 1999 to 2003, a relatively stable but high level of activity from 2004 to 2010 and decreases from 2011 to 2013 (Fig. 1E, F). Notably, outbreak activity is lower during all years in Cluster E than Cluster F, which rings Cluster F. A later period of increased outbreak activity is evident in Clusters A and D, which show increasing activity from 2005 to 2010 and 2002 to 2010, respectively. Cluster B shows only a minor increase in spruce beetle activity through time (Fig. 1B). Taken together, cluster analysis shows clear bullseye-like patterns in cluster types, where outer rings exhibit lower severity and/or time lags in mortality, suggestive of dispersal, and multiple disjunct origins, suggestive of a regional driver.

### *How do the temporal synchrony of spruce beetle activity, drought, and temperature change with distance?*

Across the SRME local synchrony of spruce beetle activity (i.e., the synchrony as distance approaches 0 km) was high (0.63) (Fig. 2A). Temporal synchrony declined

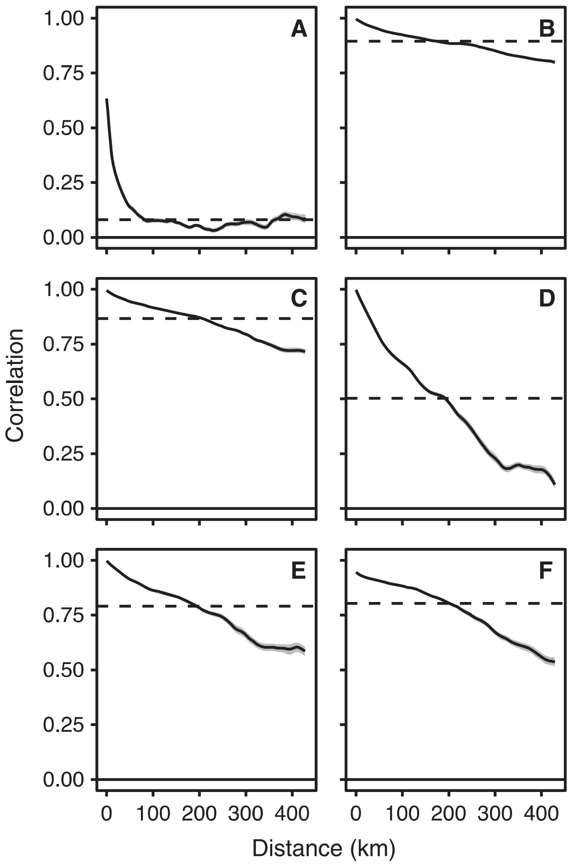

FIG. 2. Nonparametric spatial covariance function for (A) spruce beetle activity, (B) August maximum daily temperature (TMAX), (C) December minimum daily temperature (TMIN), (D) summer evapotranspiration precipitation index (SPEI), (E) 5-yr SPEI, (F) peak snow water equivalent (SWE) across the SRME. Panels A–E show data for 1999–2013 while panel F shows data for 2001–2011. Solid lines show the covariance function and show how temporal synchrony changes with increasing distance. Gray shading indicates the 95% confidence interval based on 1,000 bootstrap replications. The dashed horizontal line indicates the average correlation across the SRME (regional synchrony).

rapidly with distance and reached average correlation, i.e., regional synchrony (0.08), by 83 km (Fig. 2A). At all distances, spruce beetle activity was positively correlated, indicative of a regional driver. Peak SWE, 5-yr SPEI, Dec TMIN, and Aug TMAX were all characterized by high regional synchrony (0.80, 0.79, 0.87, 0.89), while local synchrony of Jun–Jul SPEI was high but declined more quickly with increasing distance (Fig. 2B–F).

### *How is outbreak initiation and spread associated with timing and severity of drought, temperature conditions favorable for outbreak, forest characteristics, and beetle dispersal?*

Across the SRME, spatial overlay analysis revealed outbreak occurrence was associated with drought, here SPEI and peak SWE, and that these associations depended on the proximity and extent of outbreak in the previous year (e.g., dispersal pressure; Fig. 3). Differences >10% between observed and expected values occurred more frequently for the occurrence of outbreak initiation than outbreak spread, indicating greater sensitivity to biophysical drivers when outbreaks arose from local populations or long-distance dispersal (Fig. 3). Spatial overlay analysis revealed outbreak initiation was more frequent than expected in areas with low Jun–Jul SPEI (≤−1; Fig. 3C), 5-yr SPEI (≤−0.75; Fig. 3D), and peak SWE (≤0.4; Fig. 3E). Spreading occurrence exhibited similar associations with drought (Fig. 3C–E). Affected forests appeared to occur randomly across all classes of tree cover, dominance of large trees, Aug TMAX, and Dec TMIN (Fig. 3A, B, F, G).

The RF models of spruce beetle outbreak initiation and spread confirmed the importance of dispersal pressure and drought variables. The out-of-bag (OOB) error estimates were 20% and 32% for the outbreak initiation and outbreak spread models, respectively, indicating most cases were correctly predicted. The three most important variables for predicting the occurrence of outbreak initiation were all indices of drought, while dispersal pressure, 5-yr SPEI, Dec TMIN were most important for predicting the occurrence of outbreak spread (Fig. 4A).

Partial dependence plots, which illustrate the dependence of spruce beetle outbreak occurrence on one predictor after accounting for the effects of other predictor variables, showed the occurrence of outbreak spread was more likely that unaffected forest when dispersal pressure was high (Fig. 4B). Partial dependence plots also

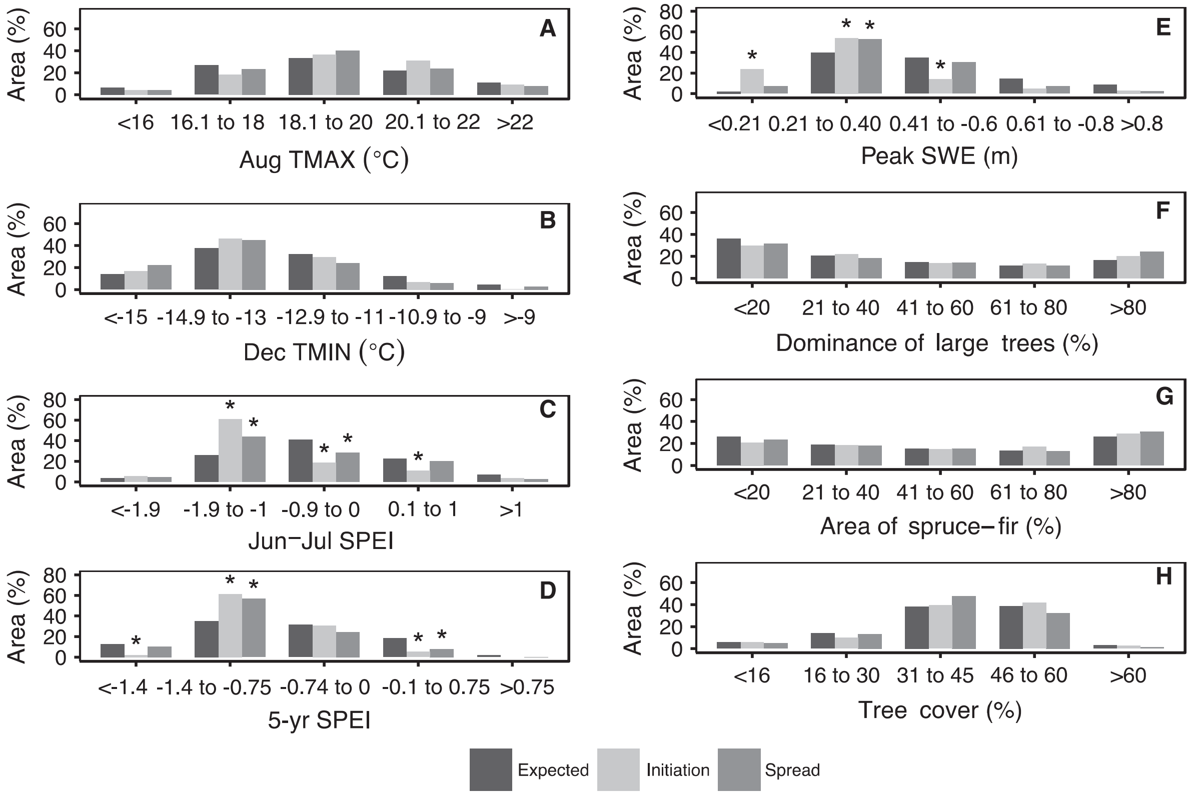

Fig. 3. Spatial overlay analysis of the occurrence of outbreak spread and initiation and biophysical variables for the SRME study area, 1999–2013: (A) August TMAX, (B) December TMIN, (C) summer SPEI, (D) 5-yr SPEI, (E) peak SWE, (F) dominance of large trees, (G) area of spruce–fir, and (H) tree cover. Dark and light gray bars indicate the observed area of outbreak spread and initiation, respectively. Black bars indicate the expected area, which was generated by calculating the percent of the landscape in each bin. Differences between observed and expected values >10% signify dependence between spruce beetle activity and the independent variable and are denoted with an asterisk. Note negative values of SPEI indicate periods where precipitation is lower than potential evapotranspiration.

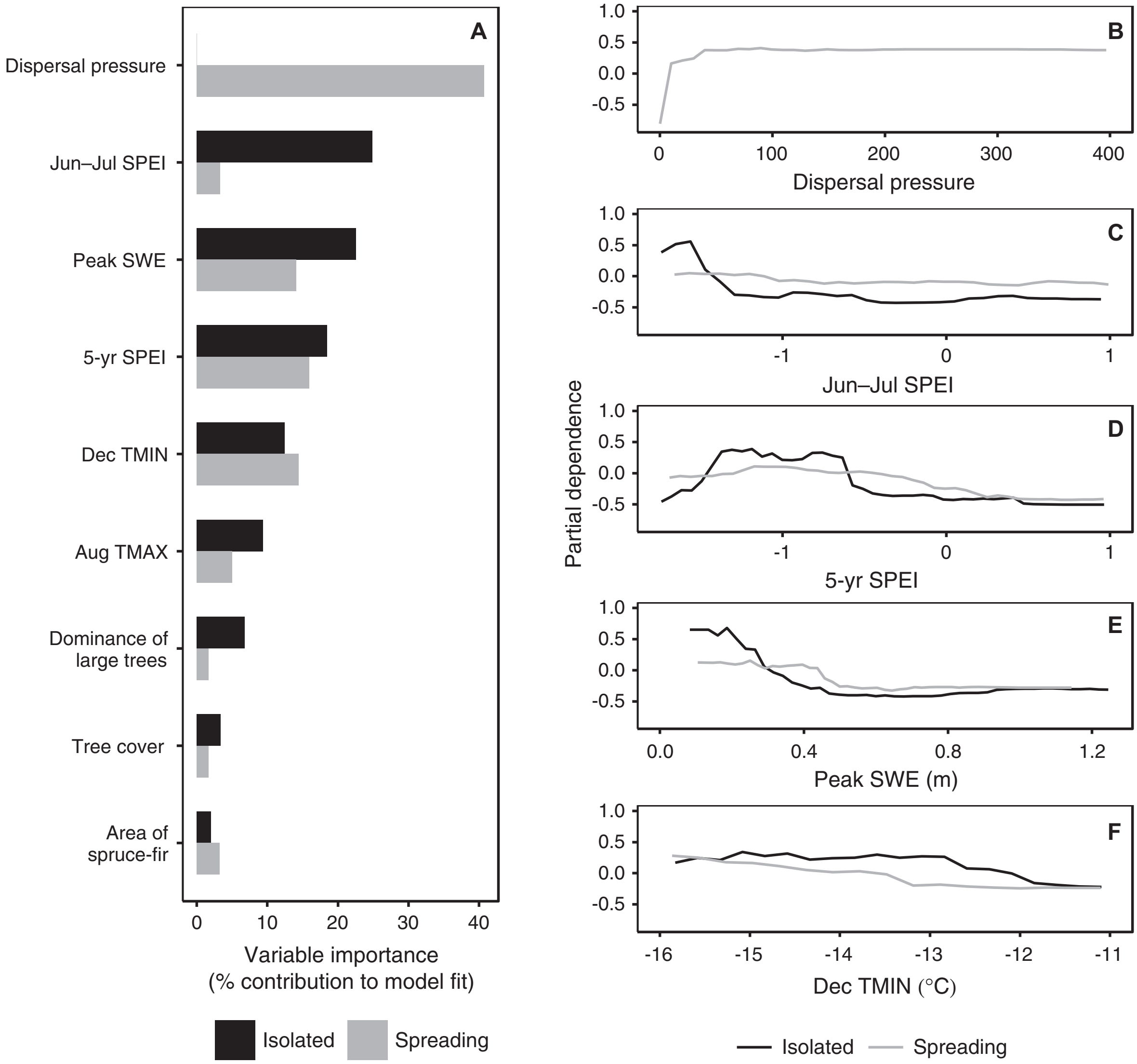

FIG 4. Results from Random Forest (RF) analysis of spruce beetle spread and initiation. (A) Variable importance plot used for predicting the occurrence of isolated and spreading spruce beetle outbreak. Variable importance is represented by the mean decrease in accuracy statistic, which is defined as the normalized difference of the classification accuracy when the data for that variable are included and when they have been randomly permutated. Values have been scaled to show the percent contribution of each variable to the overall model fit. The other panels show partial dependence plots of (B) dispersal pressure, (C) Jun–Jul SPEI, (D) 5-yr SPEI, (D) peak SWE, and (E) Dec TMIN. Partial dependence plots illustrate the relative logit contribution of the predictor variable on the probability of outbreak on after averaging out the effects of other predictor variables. Higher values indicate a greater likelihood of outbreak occurring. Rug plots at the bottom of each partial dependence plot show the distribution of the predictor variable. Negative values of SPEI indicate periods where precipitation is lower than potential evapotranspiration.

revealed outbreak initiation, and to a lesser extent, outbreak spread were favored by low Jun–Jul SPEI, 5-yr SPEI, and peak SWE (Fig. 4C–E). Contrary to expectations, outbreak spread was also favored by cold Dec TMIN (Fig. 4F).

## DISCUSSION

Here we show the initiation and spread of spruce beetle outbreak is linked to early summer drought, multiyear drought and winter drought, and the extent of nearby outbreak in the previous year (dispersal pressure). Notably, our results show that (1) spruce beetle activity initiated in multiple locations across the SRME over the 1999–2013 period, suggesting a regional driver rather than a single local trigger event; (2) over this period the temporal synchrony of spruce beetle activity was spatially synchronous at distances greater than the likely annual dispersal distance of spruce beetles, suggestive of a regional climate driver; and (3) both spatial overlay analysis and statistical modeling show outbreaks were most likely to initiate and spread into areas characterized by drought, as indicated by low Jun–Jul SPEI, 5-yr SPEI, and peak SWE values. The association between outbreak development and drought observed here supports the idea that drought may promote rapid growth of bark beetle populations by weakening tree defense mechanisms (Raffa et al. 2008). Furthermore, the stronger association between drought and outbreak initiation rather than outbreak spread suggests that drought may be most important in triggering the development of epidemic bark beetle populations.

Despite the relatively low regional synchrony of spruce beetle activity across the SRME, the high synchrony across moderate distances (e.g., $r > 0.20$ for distances $\leq$350 km) observed here is suggestive of a broad-scale driver. Consistent with previous research (Macias Fauria and Johnson 2009, Chapman et al. 2012), we found temperature variables were characterized by the greatest magnitude and slowest decline in synchrony of all variables analyzed. This high regional synchrony of temperature has been suggested to be the primary driver of synchronous mountain pine beetle outbreaks (Macias Fauria and Johnson 2009, Chapman et al. 2012). Here we show that peak SWE and 5-yr SPEI also exhibit high regional synchrony and may also be important in synchronizing spruce beetle outbreaks. Further the spatial synchrony of Jun–Jul SPEI, which declines more rapidly with increasing distance, may interact with these more broadly synchronous climate variables and bark beetle dispersal to generate the pattern of low regional and high synchrony at local to moderate distance, which we observed for spruce beetle activity.

Contrary to the expectation that warm temperatures would favor spruce beetle outbreak (Miller and Werner 1987, Hansen et al. 2001, Hebertson and Jenkins 2008), outbreak occurrence was not strongly favored by warm temperatures. While temperature and drought were not strongly correlated across the SRME (Appendix S1: Table S1), we note that warm temperatures tend to co-occur with drought. Therefore, a part of the positive effect of drought on outbreak initiation and spread may be explained by temperature-driven increases in larval development rates (Hansen et al. 2001). The association of outbreaks spread and low Dec TMIN minimum temperatures may be explained by tree species distribution patterns. Spruce is more common at cooler and wetter sites, while non-host species (e.g., lodgepole pine) are widespread at warmer sites and are less suitable for spruce beetle outbreak (Peet 2000). Subsequent analyses that new data sets depicting the relative dominance of spruce would serve to advance our understanding of the effects of temperature on outbreak spread and initiation.

The identification of low peak SWE as an important predictor of spruce beetle outbreak development is novel and suggests that the availability of snowmelt water is critical for sustaining tree defense throughout the dry hot summers. This idea is consistent with research that shows snowmelt water is important for sustaining photosynthesis throughout the growing season in Colorado's subalpine zone (Hu et al. 2010, Winchell et al. 2016). Further, non-specific tree mortality in the SRME subalpine has been linked to early season drought (Bigler et al. 2007, Smith et al. 2015). Future decreases in peak SWE may result in significant non-specific and bark beetle-driven tree mortality, particularly coupled with summer and multi-year drought.

Similar to landscape-scale analyses of mountain pine beetle outbreak in pine-dominated forests (Preisler et al. 2012), our results are consistent with a hypothesis that spruce beetle dispersal strongly affects development of an outbreak. This finding was supported by cluster analysis, which suggests spruce beetle activity spreads from areas of intense activity, and the rapid decline in temporal synchrony with increasing distance. Overlay analysis revealed that 97% of spruce beetle outbreak occurred when the neighboring pixels were affected at the previous time step (i.e., dispersal proxy >0). Furthermore, while only 3% of newly affected pixels appear to arise from endemic populations or long-distance dispersal, these local increases in spruce beetle activity are likely critical for spreading outbreak. More than 97% of isolated activity spread into the neighboring pixels at the following time step. Not surprisingly, the most important predictor for modeling spruce beetle spread was dispersal pressure. The density-dependency of spruce beetle activity observed here supports the idea that an important control on outbreak development is a positive feedback where beetles gain the ability to colonize healthy trees only at high densities (Raffa and Berryman 1983, Wallin and Raffa 2004).

In contrast to the expectation that forest characteristics drive patterns of spruce beetle outbreak (Schmid and Frye 1977), neither dominant tree size, area of spruce–fir, nor percent tree cover, were identified as important drivers of outbreak initiation and spread. The absence of this effect may be due to inaccuracy of geospatial layers and/or the absence of data describing the relative proportion of host vs. non-host trees. Alternatively, drought-driven decreases in host resistance may override the influences of stand density and tree size, as has been proposed in stand-scale studies of outbreak in the SRME (Hart et al. 2014*b*).

In conclusion, here we use a novel Landsat-based data set of spruce beetle activity across the SRME to analyze patterns of outbreak development over the 1999–2013 period. After documenting that temporal synchrony of spruce beetle activity is highly spatially dependent, we show strong associations between newly detected spruce beetle activity and drought and beetle dispersal pressure, consistent with studies in Colorado based on ADS, Forest Service forest stand inventories, historical records, and tree-ring reconstructions of spruce beetle outbreaks (Hebertson and Jenkins 2008, DeRose and Long 2012, Hart et al. 2014*a*). Notably we show that summer drought, multi-year drought and winter drought are associated with increases in the likelihood of outbreak. While many studies of future outbreak have emphasized the importance of future warming on bark beetle population dynamics (Bentz et al. 2010), our results highlight the importance of considering future drought, which affects host susceptibility to infestation. Furthermore, given that recent warming has already decreased peak SWE and the duration of snow cover across the intermountain West (Clow 2010) thereby increasing drought conditions, future alterations to precipitation regimes are likely to be critical for future spruce beetle outbreaks and drive significant change in subalpine forests.

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