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RESEARCH ARTICLE

Rocky Mountain forests are poised to recover following bark beetle outbreaks but with altered composition

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Abstract

1. Amplified by warming temperatures and drought, recent outbreaks of native bark beetles (Curculionidae: Scolytinae) have caused extensive tree mortality throughout Europe and North America. Despite their ubiquitous nature and important effects on ecosystems, forest recovery following such disturbances is poorly understood, particularly across regions with varying abiotic conditions and outbreak effects.
2. To better understand post-outbreak recovery across a topographically complex region, we synthesized data from 16 field studies spanning subalpine forests in the Southern Rocky Mountains, USA. From 1997 to 2019, these forests were heavily affected by outbreaks of three native bark beetle species (*Dendroctonus ponderosae*, *Dendroctonus rufipennis* and *Dryocoetes confusus*). We compared pre- and post-outbreak forest conditions and developed region-wide predictive maps of post-outbreak (1) live basal areas, (2) juvenile densities and (3) height

growth rates for the most abundant tree species – aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*).

3. Beetle-caused tree mortality reduced the average diameter of live trees by 28.4% (5.6 cm), and species dominance was altered on 27.8% of field plots with shifts away from pine and spruce. However, most plots (82.1%) were likely to recover towards pre-outbreak tree densities without additional regeneration. Region-wide maps indicated that fir and aspen, non-host species for bark beetle species with the most severe effects (i.e. *Dendroctonus* spp.), will benefit from outbreaks through increased compositional dominance. After accounting for individual size, height growth for all conifer species was more rapid in sites with low winter precipitation, high winter temperatures and severe outbreaks.
4. *Synthesis*. In subalpine forests of the US Rocky Mountains, recent bark beetle outbreaks have reduced tree size and altered species composition. While eventual recovery of the pre-outbreak *forest structure* is likely in most places, changes in *species composition* may persist for decades. Still, forest communities following bark beetle outbreaks are widely variable due to differences in pre-outbreak conditions, outbreak severity and abiotic gradients. This regional variability has critical implications for ecosystem services and susceptibility to future disturbances.

KEYWORDS
biotic disturbances, Compositional shifts, *Dendroctonus* spp., *Dryocoetes confusus*, structural recovery, subalpine forests

1 | INTRODUCTION

Anthropogenic climate change is altering patterns of disturbance and stand development in forested ecosystems worldwide, with likely consequences for longer-term ecosystem persistence (McDowell et al., 2020; Turner, 2010). Linked to drought, climate warming and host availability, outbreaks of native bark beetles (Curculionidae: Scolytinae) have caused extensive tree mortality throughout forests of the Northern Hemisphere since *c*. 2000 (Bentz et al., 2009; Raffa et al., 2008; Seidl et al., 2014; Sommerfeld et al., 2018). For example, in the western United States, recent beetle-caused tree mortality spanned 5% of the total forest area (Hicke et al., 2020) and killed more trees than wildfire (Berner et al., 2017). Patterns of stand development following these outbreaks have crucial implications for forest dynamics, associated ecosystem services such as nutrient cycling and wildlife habitat and susceptibility to future disturbances (Edburg et al., 2012; Harvey et al., 2014; Morris et al., 2017; Negrón & Huckaby, 2020; Saab et al., 2014; Thom & Seidl, 2016). There is a pressing need to understand forest recovery dynamics following bark beetle outbreaks because such disturbances are likely to increase in frequency and extent in response to a warming climate (Bentz et al., 2010; Kolb et al., 2016; Weed et al., 2013).

In the western United States, bark beetles – specialist herbivores that feed and reproduce within the subcortical tissue of particular host trees – are among the few biotic disturbance agents that can cause severe and widespread tree mortality (Bentz et al., 2009). Many bark beetle species persist at low population levels and target weakened trees, but when populations increase due to cross-scale interactions with biotic and abiotic drivers (i.e. 'outbreaks'), beetles can successfully colonize most hosts within a stand (Aukema et al., 2016; Boone et al., 2011). Outbreak development is complex but requires an abundance of suitable host trees, which often reflects disturbance history (Kulakowski et al., 2012; Veblen et al., 1994) and abiotic factors (Jaime et al., 2022). Given available hosts, large-scale outbreaks can occur when above-average temperatures increase overwinter insect survival and drought conditions limit host tree defences (Anderegg, Hicke, et al., 2015; Howe et al., 2022; Raffa et al., 2008). The mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins), spruce beetle (SB; *Dendroctonus rufipennis* Kirby) and western balsam bark beetle (WBBB; *Dryocoetes confusus* Swaine) caused over 70% of the recent tree mortality attributed to bark beetles in the western United States, with comparatively greater impacts in the Rocky Mountains (Hicke et al., 2020). Lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) is the primary tree host for MPB, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) is the primary host for SB, and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) is the primary host for WBBB (Bentz et al., 2009). MPB, SB and WBBB are also size-selective, preferentially targeting large, resource-rich trees during outbreaks (Johnson et al., 2014). While MPB and SB can cause rapid and severe tree mortality (e.g. rates of 20% year^{-1} within a stand; Meddens & Hicke, 2014), WBBB outbreaks are typically more gradual and occur at lower severities (e.g. <5% year^{-1}; McMillin et al., 2017); however, all three species can be present in the same forest stand.

Despite the widespread extent of recent outbreaks of MPB, SB and WBBB, their combined influence on forest stand conditions across regional extents has been largely unexplored. To address this uncertainty, we used two complementary approaches. First, we synthesized data from 16 field studies across forests of the Southern Rocky Mountains (SRM), USA (Figure 1). Surveys conducted for individual field studies provide detailed information about pre- and post-outbreak forest stand conditions but are limited in spatial extent and are unable to capture regional-scale variations in antecedent conditions, outbreak effects and topoclimate. Therefore, we combined local field surveys and broad-scale spatial data products to characterize region-wide spatial patterns of post-outbreak forest structure, composition and growth. Our specific research questions were (1) *How do initial post-outbreak stand structure and composition (one to two decades following outbreak) compare to pre-outbreak conditions?* (2) *How do post-outbreak live basal area, juvenile density and height growth rates for the most common tree species vary across bark beetle-affected subalpine forests in the SRM?* Answering these questions will shed light on the broad ecological consequences of unprecedented beetle impacts, with effects on biota and critical ecosystem services.

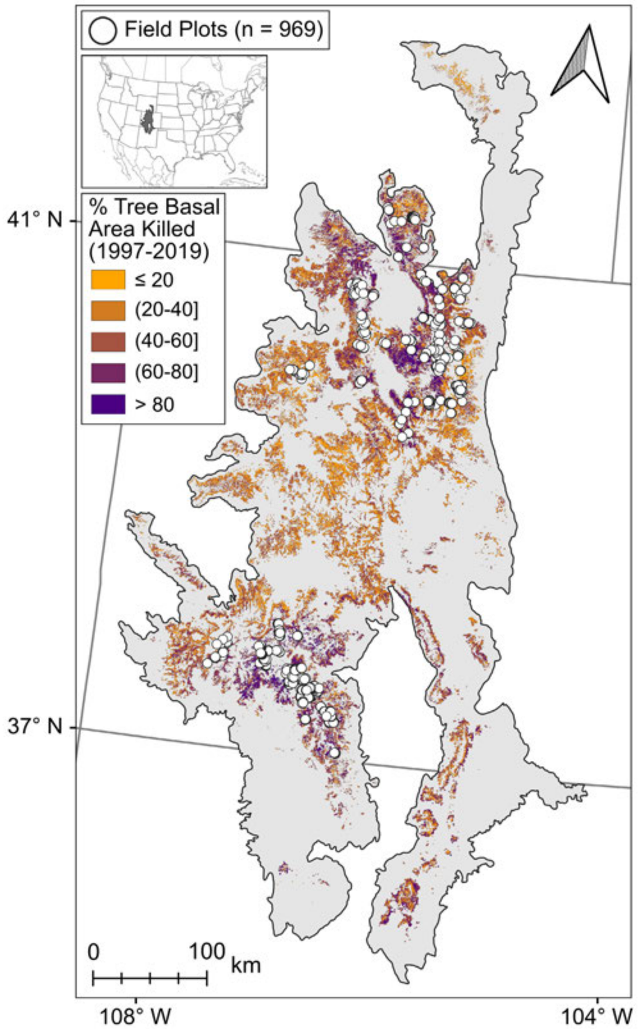

FIGURE 1 Map of the study area and sampled field plots (white circles) in the Southern Rocky Mountains, USA (EPA Level III Ecoregion #21; grey polygon). Colours (orange to purple) indicate the remotely sensed severity of bark beetle outbreaks from 1997 to 2019 (Rodman, Andrus, et al., 2021). Grey areas within the regional boundary were not analysed because they were unforested, recently logged, recently burned, outside the subalpine zone or unaffected by the most abundant bark beetle species (USFS, 2020).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study area was located in the SRM, a *c.* 145,000 km^2 region composed of mountainous terrain (ranging from 1450 to 4400 m elevation) in Colorado, southern Wyoming and northern New Mexico, USA (Figure 1). Specifically, we focused on subalpine forests (2700–3600 m; Peet, 1981; Romme et al., 2009), which comprise 28% of the total land area and 51% of the forest area in the SRM (Homer et al., 2020; Rollins, 2009). Subalpine forests in the SRM are dominated by Engelmann spruce, lodgepole pine, subalpine fir and/or aspen (*Populus tremuloides* Michx.), although five-needle pines (e.g. bristlecone pine – *Pinus aristata* Engelm., limber pine – *Pinus flexilis* James) are also important in some areas. Following widespread industrialization in the 1800s, Euro-Americans have had profound effects on SRM forests due to the forced displacement and genocide of Indigenous Peoples, high-grade logging, livestock grazing, fire exclusion in some areas and additional wildfire in others (Romme et al., 2009; Roos et al., 2021; Veblen & Donnegan, 2005; Zier & Baker, 2006). In subalpine forests, bark beetle outbreaks and severe wildfires are the most important natural disturbances, often triggered by warm temperatures and dry conditions (Baker & Veblen, 1990; Hart, Veblen, Eisenhart, et al., 2014; Sibold et al., 2006). Coinciding with a period of severe drought, at least 10,000 km^2 of subalpine forest area in the SRM experienced substantial tree mortality due to MPB, SB and WBBB from 1997 to 2019 (Rodman, Andrus, et al., 2021).

To restrict analyses to subalpine forests that were most likely to have experienced recent outbreaks of MPB, SB or WBBB, we defined the study area according to criteria developed by Rodman, Andrus, et al. (2021) (Figure 1). Specifically, we excluded areas >500 m from patches of tree mortality attributed to MPB, SB and WBBB, visually identified during US Forest Service Aerial Detection Surveys (ADS) from 1997 to 2019 (USFS, 2020), as a 500-m buffer captures most areas potentially affected by at least one of the three insects (Coleman et al., 2018). We also excluded areas without pre-outbreak forest cover using the 1992 National Land Cover Dataset (NLCD; Wickham et al., 2004) and excluded recent urban or exurban development using the 2016 NLCD (Homer et al., 2020). We further limited the study area to subalpine forests as those with ≥1 m^2 ha^{-1} total pre-outbreak basal area for the dominant subalpine conifer species (Wilson et al., 2013). Finally, we ensured that observed changes in forest conditions were related to bark beetles rather than other disturbances (e.g. fire and harvest) by excluding areas with recorded fires (Eidenshink et al., 2007; GeoMAC, 2020) or timber harvests (Caggiano, 2017; USFS, 2020) that occurred from 1996 to 2019. The extent of our final study area was 33,273 km^2 at a 30-m grain size (23.0% of the total SRM).

2.2 | Field data collection

We compiled field datasets that were collected for 16 studies of bark beetle effects on subalpine forests throughout the SRM (Andrus, Chai, et al., 2021; Andrus, Hart, & Veblen, 2020; Audley et al., 2020; Carlson et al., 2020; Carter et al., 2022; Chapman, Unpublished Data; Coop et al., Unpublished Data; Fornwalt et al., 2018; Gill et al., 2017; Harvey et al., 2021; Morris et al., 2022; Nigro et al., 2022; Pappas et al., 2020; Redmond & Kelsey, 2018; Rhoades et al., 2020; Schapira, Stevens-Rumann, Shorrock, Hoffman, & Chambers, 2021). This combined dataset includes 969 field plots with nearly 40,000 records of trees (≥3 m in height) and saplings (≥1.4 m and <3 m), tallies of over 40,000 juveniles (<1.4 m) and height growth rates for nearly 2000 saplings and juveniles (Figure 1; Appendix S1). In the field, crews identified the species and status [i.e. live, recently dead (1990s to 2010s) or older dead (pre-1990s)] of all trees and saplings. We excluded older dead from all analyses as these trees were assumed to have died before our study period, and our focus was on recent beetle-caused tree mortality (following Harvey et al., 2021). Field protocols, including plot sizes and sampling schemes, varied slightly among studies (Tables S1.1–S1.3); thus, we standardized datasets such that tree, sapling and juvenile data were directly comparable (Appendix S1).

2.3 | Data processing and analysis

2.3.1 | Question 1 – Comparing pre- and post-outbreak conditions in field plots

To better understand outbreak-driven changes in forest conditions, we assessed structure, species composition and expected forest trajectories on a subset of field plots (*n* = 747) that contained species-level information for each of the most abundant tree species. To compare pre- and post-outbreak size structures, we developed composite diameter distributions of live and dead trees/saplings at the time of field surveys and calculated the quadratic mean diameter (QMD; Curtis & Marshall, 2000) for live trees in pre- and post-outbreak stands. To quantify shifts in species dominance across field plots, we identified the pre- and post-outbreak dominant species on each plot, defined here as the tree species with the greatest live basal area. Relative dominance within a stand can change over time due to interspecific differences in growth, recruitment and mortality. Thus, we modelled forest dynamics over a 30-year simulation period to assess the stability of post-outbreak species composition using the Forest Vegetation Simulator (FVS), a widely applied stand-scale simulation model of forest growth and mortality (Dixon, 2002; Appendix S2). In FVS simulations, we based initial forest conditions on post-outbreak tree lists that included all surveyed trees ≥5 cm in height; we assumed constant climatic conditions, no subsequent disturbances and no additional regeneration beyond existing juveniles in each stand. Finally, to characterize structural recovery potential in each field plot, we calculated a ratio of the measured post-outbreak density (stems ha^{-1}) of all trees ≥5 cm in height (i.e. trees, saplings and juveniles) to the pre-outbreak density of trees ≥1.4 m in height (i.e. trees and saplings only; hereafter 'density ratio'), similar to the recruit/adult ratio of Carnicer et al. (2021). We inferred that plots with density ratios <1 would require additional tree establishment to recover to pre-outbreak densities, while plots with values ≥1 were better positioned for structural recovery through the recruitment of existing juveniles.

2.3.2 | Question 2 – Predicting post-outbreak conditions across the Southern Rocky Mountains

To develop predictive models of post-outbreak conditions, we used field data (*n* = 969 plots) to create species-specific response variables of (1) live basal areas for all trees and saplings, (2) juvenile densities and (3) individual height growth rates for saplings and juveniles. To do so, we summarized plot-level data describing post-outbreak live basal area (m^2 ha^{-1}) and juvenile density (stems ha^{-1}) for each of the most common tree species in subalpine forests of the SRM (i.e. aspen, Engelmann spruce, lodgepole pine and subalpine fir; Peet, 1981; Romme et al., 2009). At the individual-tree level, we summarized height growth rates (average cm yr^{-1}) for the three dominant coniferous species based on methods used in individual studies – that is, internode measurements of annual growth (Andrus, Hart, & Veblen, 2020; Harvey et al., 2021; Rhoades et al., 2020) or repeated surveys (Pappas et al., 2020) – across a subset of field plots (*n* = 254) that spanned the SRM. Height growth rates of aspen were excluded from our analyses due to insufficient sample size and a growth form that precludes the use of internode measurements. Because individual traits and species identity can affect tree response to environmental conditions (Clark et al., 2021), we obtained the post-outbreak stem height and species of measured juveniles and saplings from field data as potential covariates in the growth model.

We used spatially explicit datasets to derive potential predictors of each species-specific response variable (Table 1, Appendix S3). We expected that post-disturbance conditions would be strongly influenced by the pre-disturbance state (Johnstone et al., 2016). Thus, we obtained pre-outbreak species basal areas from US Forest

TABLE 1 Variables used to predict forest conditions following recent bark beetle outbreaks in the Southern Rocky Mountains, USA. The data sources or references for methods of calculation are included in the description of each variable

			Response Variable		
Category[a]	Predictor	Description	Live BA[b]	Juv. Density[b]	Ht. Growth[b]
Climate	AET	Annual actual evapotranspiration from water balance models in the 1981–2010 period (Rodman et al., 2020). 250-m		x	x
	CWD	Annual climatic water deficit from water balance models in the 1981–2010 period (Rodman et al., 2020). 250-m		x	x
	Jan TMin	Average minimum daily temperature from January 1981–2010 (Oyler et al., 2015). 250-m		x	x
	July TMax	Average maximum daily temperature from July 1981–2010 (Oyler et al., 2015). 250-m		x	x
	Summer Ppt	Average total precipitation May 1–October 31, 1981–2010 (PRISM Climate Group, 2022). 250-m		x	x
	Winter Ppt	Average total precipitation November 1–April 30, 1981–2010 (PRISM Climate Group, 2022). 250-m		x	x
Pre-outbreak conspecific basal area	Species BA - Pre	Pre-outbreak species basal area in 2002, before the onset of most outbreaks. Derived from an existing spatial dataset (USFS, 2021). 30-m	x	x	
	Focal BA - Pre	Pre-outbreak species basal area from 2002 in the surrounding area, using a focal sum with inverse distance squared weighting (Coop et al., 2019). Calculated in 300, 600, and 900 m window sizes to summarize short, intermediate and long-range propagule pressure. 30-m		x	
Pre-outbreak forest cover	Forest cover - Pre	Percent forest cover 2000–2001, before the onset of most outbreaks. Calculated as the mean of two existing Landsat-derived products (Hansen et al., 2013; Homer et al., 2007). 30-m	x	x	x
Remotely sensed greenness	EVI2 Amp	The difference between maximum and minimum values of the two-band enhanced vegetation index (EVI2) during the 2019 growing season. Calculated using modelled time series of the Harmonized Landsat-Sentinel (HLS) and Visible Infrared Imaging Radiometer Suite (VIIRS) products (Zhang et al., 2020). 30-m	x	x	x
	EVI2 Max	The maximum EVI2 throughout the 2019 growing season, calculated from modelled HLS/VIIRS time series (Zhang et al., 2020). 30-m	x	x	x
	EVI2 SD	The standard deviation of EVI2 during the 2019 growing season, calculated from modelled HLS/VIIRS time series (Zhang et al., 2020). 30-m	x	x	x

(Continues)

TABLE 1 (Continued)

Category[a]	Predictor	Description	Response Variable Live BA[b]	Juv. Density[b]	Ht. Growth[b]
Remotely sensed phenology	SOS	Start date of the 2019 growing season, calculated using a hybrid piecewise logistic model of HLS/VIIRS time series of EVI2 (Zhang et al., 2020). 30-m	x	x	x
	POS	Peak date of the 2019 growing season, calculated using a hybrid piecewise logistic model of HLS/VIIRS time series of EVI2 (Zhang et al., 2020). 30-m	x	x	x
	EOS	End date of the 2019 growing season, calculated using a hybrid piecewise logistic model of HLS/VIIRS time series of EVI2 (Zhang et al., 2020). 30-m	x	x	x
	LOS	Length of the 2019 growing season, calculated as EOS minus SOS (Zhang et al., 2020). 30-m	x	x	x
Remotely sensed outbreak severity	Outbreak Severity	Cumulative basal area mortality (% of pre-outbreak total for all species) attributed to bark beetle attack 1997–2019, based on Landsat time series with field validation (Rodman, Andrus, et al., 2021). 30-m	x	x	x
Soil	Soil AWC	Available water capacity in the top 200 cm of the soil. The product of depth to bedrock and fractional water capacity (Chaney et al., 2016). 30-m		x	x
Terrain	HLI	Continuous heat load index. An estimate of the intensity of terrain-driven solar heating that combines slope angle, latitude and aspect (McCune & Keon, 2002; Theobald et al., 2015). 10-m		x	x
	TPI	Topographic position index. The elevation of a site relative to the surrounding area. Calculated as separate variables in 150, 450 and 1350-m window sizes (Weiss, 2001). 10-m		x	x
	TWI	Topographic wetness index. An estimate of topographic moisture, calculated as log(upstream catchment area/slope; Beven & Kirkby, 1979). 30-m		x	x
Individual factors[c]	Height	The vertical distance from the root collar to the tip of the terminal bud. Tree-level			x
	Species	Species identity of the measured individual. Tree-level			x

[a] Categories are related groups of variables that were used to limit multicollinearity in model selection.

[b] An 'x' in this column indicates that a predictor was tested for potential inclusion in corresponding models.

[c] 'Individual factors' were predictors obtained from field data, while predictors in all other categories were spatially continuous datasets used to make region-wide predictions.

Service Individual Tree Species Parameter Maps (ITSPM), which were modelled from Forest Inventory and Analysis plots, Landsat imagery, climate, terrain and soil data (USFS, 2021) and included them as predictors in our models. As a predictor of juvenile densities, we also calculated the species-specific densities of seed trees from ITSPM maps using a distance-weighted focal sum (Coop et al., 2019) to account for dispersal from the surrounding area. Because climate, terrain and soil data were already used to make ITSPM maps, we did not include these variables as predictors of post-outbreak live basal area. However, juveniles can have a different environmental niche than conspecific adults (Bell et al., 2014; Dobrowski et al., 2015). Therefore, we used several existing climate, terrain and soil datasets as predictors of juvenile densities and height growth rates. These predictors included annual water balance metrics (actual evapotranspiration and climatic water deficit), seasonal precipitation totals (summer and winter precipitation), extreme temperatures from the warmest and coldest months (July maximum and January minimum), terrain proxies for moisture availability (topographic position index, topographic wetness index, heat load index) and soil available water capacity (Appendix S3) – variables known to influence tree regeneration in SRM forests (Andrus et al., 2018; Rodman et al., 2020; Schapira, Stevens-Rumann, & Shorrock, 2021).

We expected that total forest cover would be related to post-outbreak tree basal area, juvenile abundance and growth (Andrus, Hart, & Veblen, 2020; Pettit et al., 2019); therefore, we developed maps of pre-outbreak canopy cover for potential inclusion in all models. Similarly, because post-outbreak live basal area is a function of outbreak severity and mature trees influence conditions experienced by juveniles (Pelz et al., 2018; Veblen et al., 1991), we used existing maps of the severity of 1997–2019 outbreaks, derived from Landsat time series and field data (Rodman, Andrus, et al., 2021) as a potential predictor of each response. To describe patterns of spectral reflectance indicative of post-outbreak vegetation on a site, we also developed remotely sensed estimates of post-outbreak greenness and phenology to improve predictions of each species-specific response. Such variables have been effectively used to predict forest structure and composition (e.g. differentiating evergreen vs. deciduous) because of their associations with total vegetation biomass, primary productivity and seasonal growth patterns (Potapov et al., 2021; Wilson et al., 2012). Specifically, we followed the methods of Zhang et al. (2020) to develop high-resolution maps of post-outbreak greenness (maximum, amplitude and standard deviation of greenness) and the timing of important phenological events (start of season, peak of season, end of season, length of season) using time series of the two-band enhanced vegetation index (EVI2; Jiang et al., 2008). Because spatial predictors were created at a range of grain sizes (10 to 250 m), we aligned and reprojected each dataset to a standard 30-m reference grid. Finally, we extracted values of each spatial predictor at the locations of field plots for use in subsequent analyses.

Using field-derived responses and predictors derived from spatial data products (Table 1), we developed statistical models to predict post-outbreak live basal area, juvenile density and height growth rates of the most common tree species and used these models to make 30-m maps of each response throughout the study area. For each response, we used GLMMs (Bolker et al., 2009) with a random intercept term of 'contributor' to account for study design differences. Live basal areas and juvenile densities of each species were zero-inflated, so we used two-stage GLMMs (i.e. 'hurdle models'; Zuur et al., 2009). We used binomial error structures for all presence models and gamma (live basal area) or zero-truncated negative binomial (juvenile density) error structures for conditional abundance models. For juvenile densities, we predicted the count of juveniles on a plot and included an offset term of 'log(plot size)' to control for variation in sampling effort. To model height growth rates, we developed a single hierarchical GLMM (gamma error structure) with the average annual growth of each individual as the response. In addition to plot-level predictors considered for inclusion in models of juvenile density and post-outbreak live basal area, we included species identity and individual height as potential predictors in models of individual height growth (Table 1). To account for the dependence of height growth rates among multiple individuals within each plot, we included a random intercept term of plot nested within contributor.

To limit overfitting and improve predictive performance in unsampled areas, we used a spatially stratified cross-validation procedure for model selection (Meyer et al., 2019). First, we performed a spatial cluster analysis with the K-medoids algorithm (Kaufman & Rousseeuw, 2005) to partition field plots into 10 clusters based on their spatial locations. Using these clusters, we performed 10-fold cross-validation to assess model performance with different sets of predictors. To limit issues of multicollinearity in model selection, we combined predictors into nine groups that were expected to relate to response variables in unique ways (Table 1). From each group, we added up to two uncorrelated predictors [i.e. $-0.5 <$ Spearman's rho $(\rho) < 0.5$] that led to the highest predictive accuracy in cross-validation (i.e. 'initial models'). Where appropriate, we included non-linear relationships or two-way interaction terms based on a priori expectations (Appendices S3 and S4). To ensure realistic model predictions, we used post hoc variable removal to exclude terms that did not match ecologically informed expectations of relationships between predictors and responses (Table S3.1). We fit GLMMs using the SPAMM package (Rousset & Ferdy, 2014), assessed the distribution of model residuals using the 'ncf' (Bjornstad, 2019) and DHARMA packages (Hartig, 2018) and tested for multicollinearity using the PERFORMANCE package (Lüdecke et al., 2021) in R (R Core Team, 2021). When necessary to account for spatial dependence of model residuals (i.e. Moran's $I > 0.05$ and notable issues in spline correlograms of model residuals), we included a spatial random effect term based on plot coordinates (Rousset & Ferdy, 2014). We calculated variable importance by permuting each predictor 100 times and assessing the mean decrease in accuracy relative to intact data (Breiman, 2001).

Using final GLMMs and the RASTER package (Hijmans, 2015) in R, we made predictions of each response throughout the study area. For height growth, we developed separate predictions for each tree species, assuming a 1-m stem height, thereby mapping regional variation in growth attributed to species identity, forest structure and abiotic factors. To limit spatial predictions to areas with the likely occurrence of each tree species, basal area predictions were restricted to 30-m cells with ≥0.1 m^2 of pre-outbreak conspecific basal area ha^{-1} based on ITSPM maps, while juvenile density and growth predictions were restricted to cells within 500 m of these areas. This 500-m threshold retained >95% of juvenile presences of each species in field plots while removing errant predictions outside of each species' range. We used the resultant maps from these spatial predictions to calculate the percentage of the study area where each species had the greatest basal area, juvenile density or height growth rates. To assess region-wide shifts in species dominance, we also compared our post-outbreak basal area maps with pre-outbreak maps from ITSPM.

3 | RESULTS

3.1 | Question 1 – Comparing pre- and post-outbreak conditions in field plots

Recent bark beetle outbreaks drove changes in tree size distributions across field plots, reducing the average diameter of live trees and saplings (i.e. QMD; Figure 2). Due to selective mortality of large trees, plot-level QMDs declined by 28.4% [mean (SE) = 5.6 cm (0.2)] following outbreaks, although changes differed among species. Driven by SB- and MPB-caused tree mortality, QMDs of live Engelmann spruce [22.4 (pre-) vs. 14.6 cm (post-outbreak)] and lodgepole pine [18.5 (pre-) vs. 13.6 cm (post-outbreak)] substantially declined following outbreaks. In contrast, QMDs of live aspen [10.1 (pre-) vs. 9.6 cm (post-outbreak)] and subalpine fir [14.3 (pre-) vs. 13.3 cm (post-outbreak)] showed comparatively little change (Figure 2a). Interspecific differences in mortality rates drove shifts in the dominant tree species on 27.8% of field plots following outbreaks (Figure 2b). For example, Engelmann spruce declined in dominance from 46.6% to 30.3% of field plots, and lodgepole pine declined from 39.2% to 33.2%. In contrast, aspen increased in dominance from 2.1% to 5.5% of field plots, and subalpine fir increased from 10.4% to 28.5%. Using FVS model simulations, we predicted that these outbreak-driven shifts in species dominance would persist through upcoming decades after accounting for interspecific differences in juvenile recruitment, growth and density-dependent mortality; pine (24.2% of plots) demonstrated further declines, spruce showed little change (32.2%), and aspen (10.2%) and fir (32.0%) showed additional increases (Appendix S2; Figure 2b). Within field plots, outbreak-driven mortality of all trees and saplings was exceedingly rare (0.8% of plots; Figure 2b). While the density ratio varied widely (Figure 3a), 82.1% of plots had a ratio greater than one (Figure 3b), suggestive of recovery to pre-outbreak forest densities in most areas.

3.2 | Question 2 – Predicting post-outbreak conditions across the Southern Rocky Mountains

Post-outbreak basal areas of aspen, Engelmann spruce, lodgepole pine and subalpine fir varied widely across the SRM (Figure 4). Overall, aspen basal area was most abundant at low elevations in the western SRM (Figure 4b), Engelmann spruce basal area was abundant at high elevations throughout the SRM (Figure 4c), lodgepole pine was abundant at low elevations in the northern SRM (Figure 4d) and subalpine fir was abundant at intermediate to high elevations in the northern and western SRM (Figure 4e). All four species were positively associated with pre-outbreak species basal area and negatively associated with remotely sensed outbreak severity (Figure 4a; Figures S4.1–S4.4). Aspen had high basal areas in sites with a start of the growing season (SOS) around May 30 and a length of the growing season (LOS) of *c.* 150 days, with high variation in greenness (EVI2 Amp; Figure S4.1). Engelmann spruce, on the other hand, was associated with a later SOS (i.e. after July 1; Figure S4.2). Lodgepole pine was prevalent in areas with an early SOS (i.e. before May 15), lower EVI2 Amp and higher pre-outbreak forest cover (Figure S4.3). Subalpine fir was positively associated with a later SOS (i.e. after July 1), a shorter LOS (*c.* 130 days), intermediate greenness (EVI2 Max of ca. 0.3) and high pre-outbreak forest cover (Figure S4.4). Models of species presence [area under the curve (AUC) range 0.76–0.89] and conditional abundance [Spearman's rho (ρ) range 0.31–0.46] were strongly related to each response based on spatially stratified cross-validation (Table S4.1). Based on region-wide predictive maps, Engelmann spruce declined in dominance from 34.0% to 25.8% of the study area following outbreaks, while lodgepole pine declined from 25.3% to 20.8% (Tables S4.2 and S4.3). In contrast, aspen dominance increased from 22.8% to 23.0% of the study area, while subalpine fir increased from 17.9% to 28.4%.

We predicted high juvenile densities of aspen (dominant in 44.9% of the study area) and subalpine fir (39.1%) across much of the study area, and these species were particularly common in the western and northwestern SRM, respectively (Figure 5b,e; Table S4.4). In contrast, Engelmann spruce (10.8% of the study area) and lodgepole pine (5.3%) had generally low juvenile densities, although they were locally abundant throughout high elevations of the SRM (spruce) or in the northern SRM (pine; Figure 5c,d). Overall juvenile densities were greatest at mid- to high-elevation sites in the subalpine zone of SRM. As expected, juveniles of each species were associated with high pre-outbreak species basal areas in the surrounding area (Focal BA; Figure 5a). Juvenile aspen were abundant at sites with low or intermediate climatic water deficit (CWD; *c.* 300 mm), low actual evapotranspiration (AET), low July maximum temperature (July TMax) and high heat load index (HLI; i.e. southwesterly aspects), together indicative of mid-elevation areas with high insolation (Figure S4.5). Aspen was also associated with high EVI2 Amp and moderate pre-outbreak forest cover (i.e. 50%). Juvenile Engelmann spruce were prevalent in sites with high AET, low January minimum temperature (Jan TMin), intermediate July TMax (*c.* 21°C), low HLI and low topographic position index (TPI; i.e. valley bottoms), suggestive of cold, wet areas and protected topography (Figure S4.6). Engelmann spruce was also associated with intermediate EVI2 Max (*c.* 0.3) and low pre-outbreak forest cover. Juvenile lodgepole pine were abundant at high CWD, low AET, high July TMax, low Jan TMin and low pre-outbreak forest cover, indicative of harsh, dry, open sites (Figure S4.7). Juvenile subalpine fir were prevalent in sites with intermediate CWD (*c.* 300 mm), Jan TMin (*c.* −12°C) and July TMax (*c.* 22°C), as well as low HLI, indicative of wet, mid- to high-elevation sites (Figure S4.8). Subalpine fir was also associated with low EVI2 Amp, intermediate EVI2 Max (*c.* 0.3) and earlier EOS (around September 15th). Models of juvenile presence (AUC range 0.82–0.91) and abundance (ρ range 0.30–0.55) performed well for each species (Table S4.1).

Post-outbreak conifer height growth rates varied throughout the SRM, with lodgepole pine being the fastest-growing species in 46.3% of the study area, followed by subalpine fir (46.1%) and Engelmann spruce (7.6%; Figure 6; Table S4.5). Overall, lodgepole pine growth was most rapid at lower elevations in the northern SRM, while subalpine fir was most rapid at high elevations in the western and southern SRM (Figure 6c,d). Unsurprisingly, stem height

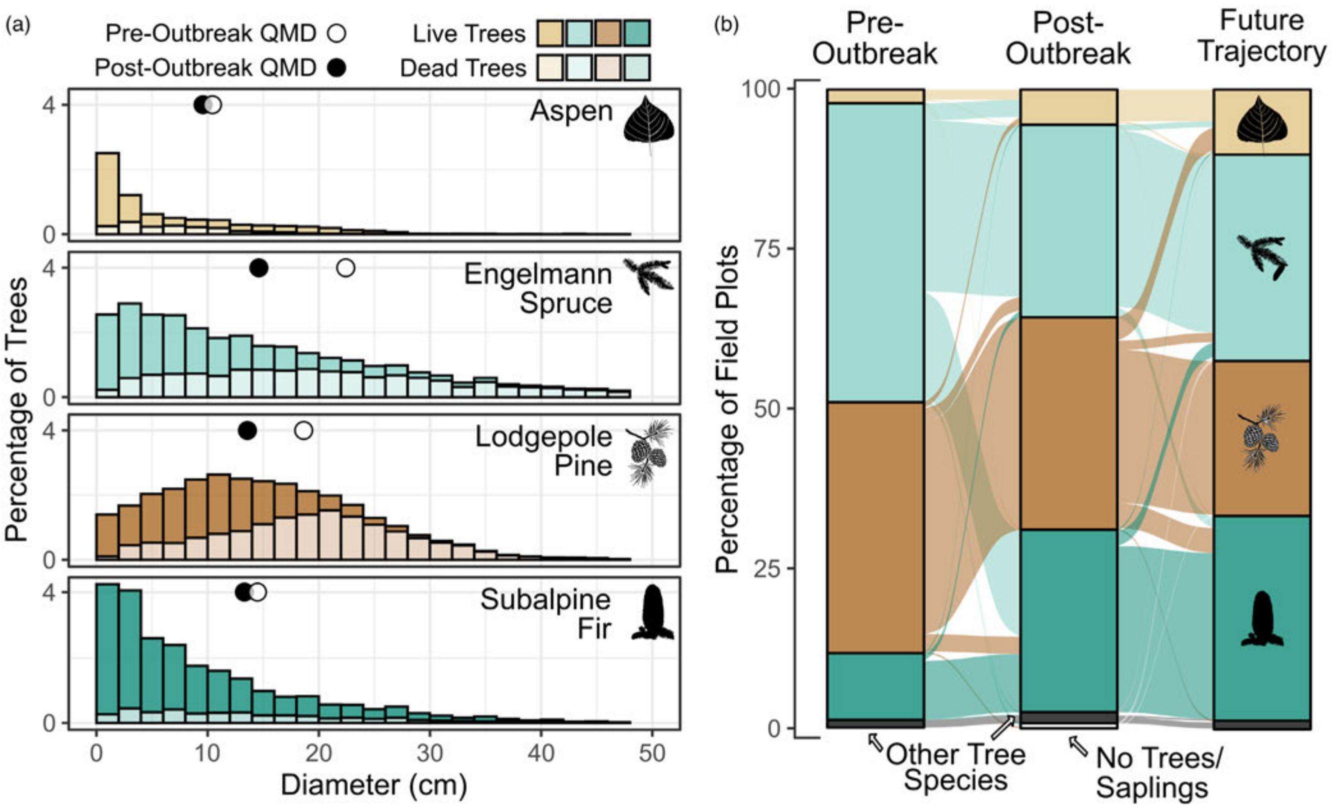

FIGURE 2 Shifts in live (a) size structure and (b) species composition in field plots affected by bark beetle outbreaks throughout subalpine forests in the Southern Rocky Mountains, USA. In (a), circles give the quadratic mean diameter (QMD) for each species before (1990s) and after (2010s) major outbreaks, including all trees (≥3 m in height) and saplings (≥1.4 m and <3 m). In (b), stacked bars show the percentage of field plots in which a species was dominant (i.e. greatest live basal area) pre-outbreak, post-outbreak and in the future (based on 30-year runs of the Forest Vegetation Simulator); ribbon widths show the portion of plots following each trajectory. 'No Trees/Saplings' plots had no individuals ≥1.4 m in a given period.

was the strongest predictor of individual height growth rates (i.e. >75% relative importance), with tall individuals showing the greatest post-outbreak growth (Figure 6a; Figure S4.9). However, after accounting for individual stem height, growth rates for all species were influenced by climate and site factors. Overall, height growth was greatest on sites with low winter precipitation (Winter Ppt) and high Jan TMin. Relationships between Winter Ppt and growth were consistent across species, although there was an interaction between species and Jan TMin, indicating that lodgepole pine growth had a stronger response to Jan TMin than did spruce or fir. Remotely sensed outbreak severity had a strong positive association with growth rates, while soil available water capacity (Soil AWC) and EVI2 Amp had weak positive associations. The height growth model was highly accurate based on cross-validation ($\rho = 0.79$; Table S4.1).

4 | DISCUSSION

By comparing pre- and post-outbreak forest communities using field surveys and developing region-wide predictive maps of post-outbreak forest conditions, we demonstrated that structural recovery is likely throughout most beetle-affected subalpine forests in the SRM, but shifts in tree species composition may endure, particularly in the absence of subsequent disturbances. We found that MPB and SB caused disproportionate mortality of larger lodgepole pine and Engelmann spruce, which is consistent with findings from more localized studies (Bakaj et al., 2016; Bleiker et al., 2003; Hart, Veblen, & Kulakowski, 2014; Johnson et al., 2014; Perovich & Sibold, 2016; Rhoades et al., 2017) and with our general understanding of bark beetle ecology (Fettig et al., 2014; Jenkins et al., 2014; McMillin et al., 2017). However, our study advances the understanding of outbreak-driven forest change by leveraging extensive field data and cutting-edge spatial data products to illustrate the effects of three co-occurring bark beetle species on stand structure and composition across a region with substantial variation in pre-outbreak forest conditions, outbreak severities and abiotic settings. Region-wide variation in these factors has led to a broad range of forest conditions throughout the SRM.

4.1 | Bark beetle caused changes in forest structure and composition

Following outbreaks, we observed a 28.4% reduction in live QMD in field plots, with the greatest declines for Engelmann spruce and

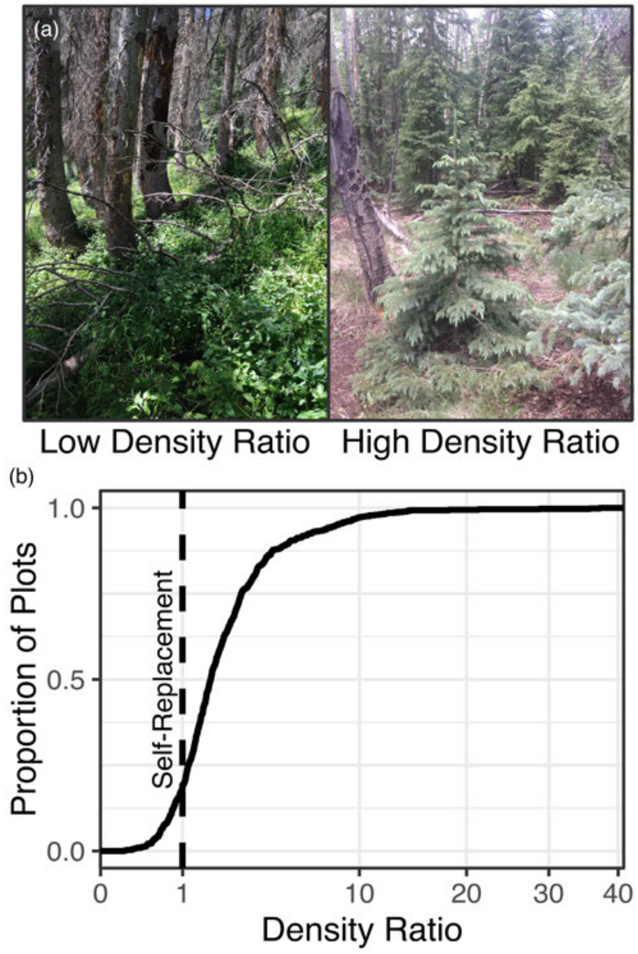

FIGURE 3 Variability in post-outbreak recovery potential across field plots in subalpine forests in the Southern Rocky Mountains, USA. Recovery potential is summarized using the density ratio – the post-outbreak density of all trees (≥3 m in height), saplings (≥1.4 m and <3 m) and juveniles (<1.4 m) divided by the pre-outbreak density of trees and saplings. In (a), photos are examples of field plots with low (0.1; left) and high (13.2; right) density ratios following bark beetle outbreaks. In (b), the cumulative distribution of the density ratio is given across all field plots, where the vertical dashed line is centered on 1; values greater than 1 are suggestive of potential self-replacement for any dead trees or saplings. Note that the x-axis breaks in (b) are on a nonlinear scale to facilitate interpretation.

lodgepole pine (Figure 2a). Recent bark beetle outbreaks throughout the SRM have led to broad-scale declines in forest basal area (Figure 1; Rodman, Andrus, et al., 2021), primarily through beetle-caused tree mortality of larger trees (i.e. ≥20 cm DBH; Audley et al., 2020; Hart, Veblen, & Kulakowski, 2014; Harvey et al., 2021). Despite strong defences against colonization (Boone et al., 2011), large trees are the preferred hosts for MPB and SB because they provide an abundant food source (i.e. high thickness and volume of phloem), which enhances insect reproductive potential and survival (reviewed in Fettig et al., 2014; Schmid & Frye, 1977). Disproportionate mortality of large trees, which produce more abundant seeds (Andrus, Harvey, et al., 2020; Qiu et al., 2021), may influence forage resources for wildlife species (Ivan et al., 2018) or leave forests vulnerable to future disturbances. For example, forests dominated by Engelmann spruce and subalpine fir, species that rely on seed dispersal from live trees to recolonize disturbed sites, often shift to non-forest vegetation or alternative compositions following beetle outbreaks and severe secondary disturbances such as wildfire (Andrus, Hart, et al., 2021; Carlson et al., 2017; Nigro et al., 2022). Lodgepole pine, on the other hand, might be less sensitive to short-interval beetle outbreaks and wildfire (Harvey et al., 2014; Talucci & Krawchuk, 2019) because seeds from serotinous cones can remain viable for 20–30 years after tree death (Aoki et al., 2011; Teste et al., 2011). Large trees also comprise the majority of live forest biomass and play a critical role in nutrient cycling (Lutz et al., 2018); however, carbon and nitrogen cycling typically stabilize within a few years of outbreak occurrence due to compensatory vegetation responses (Frank et al., 2014; Rhoades et al., 2013; Romme et al., 1986).

Despite widespread mortality of large trees, we found that most field plots (82.1%) were likely to recover to pre-outbreak densities without any new tree establishment, illustrating that most subalpine forests in the SRM have a high potential for structural recovery following recent bark beetle outbreaks (Figure 3b). Several field-based and model-based studies have also illustrated the potential for structural recovery in subalpine forests of the SRM following outbreaks through the release of non-host species and advance regeneration (Andrus, Hart, & Veblen, 2020; Collins et al., 2011; Veblen et al., 1991). Furthermore, while the remaining 17.9% of our plots were on a trajectory towards reduced tree densities following recent outbreaks, these areas may still recover to pre-outbreak densities over time. Other studies have noted substantial new seedling establishment following recent MPB and SB outbreaks in the western US (Pelz et al., 2018; Pettit et al., 2019; Talucci & Krawchuk, 2019), which could also support structural recovery in low-density areas. Although rare in our study, other research has demonstrated that outbreak-driven declines in tree density or conversions to non-forest communities are most likely in monospecific stands composed of larger trees (Andrus, Hart, & Veblen, 2020), which are most susceptible to severe outbreaks (Hart et al., 2015; Windmuller-Campione et al., 2021). Indeed, species diversity, structural variability and spatial heterogeneity have long been theorized to promote stability and adaptive capacity in ecological systems (Koontz et al., 2020; Tilman & Downing, 1994; Turner, 2010).

Using field surveys and predictive maps, we identified region-wide outbreak-driven shifts in species composition towards aspen and subalpine fir (Figure 2b; Tables S4.2 and S4.3). These findings are consistent with past research identifying stand-scale shifts in tree species composition following bark beetle outbreaks (DeRose & Long, 2007; Diskin et al., 2011; Kayes & Tinker, 2012; Perovich & Sibold, 2016). Although we found outbreak-driven increases in aspen dominance (Figure 2b), and an ability of aspen to tolerate warmer sites (e.g. increased juvenile abundances at high HLI and relatively high CWD; Figure S4.5), we expect that such relationships may be counteracted by other important pressures on the species. For example, aspen recruitment into the forest canopy is reduced by

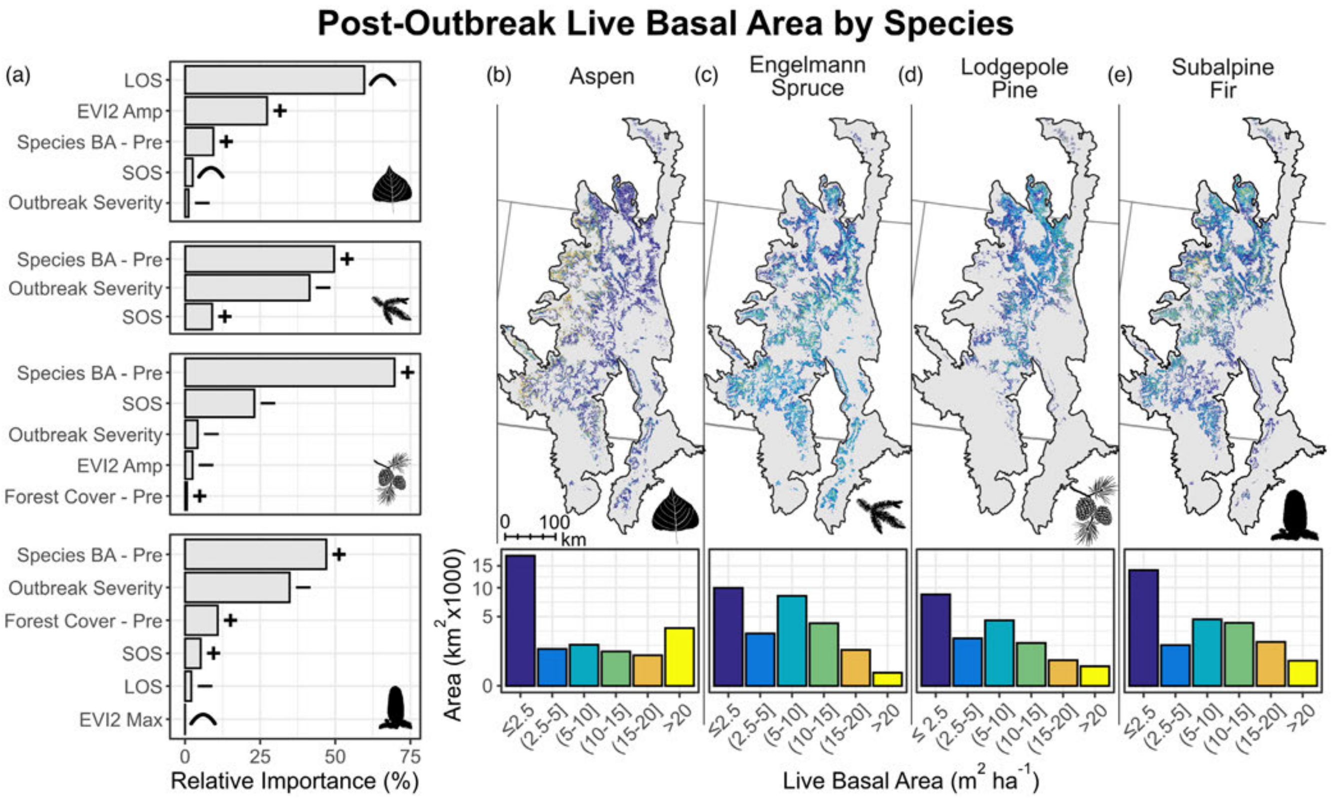

FIGURE 4 Results from generalized linear mixed models of post-outbreak live basal area of four common tree species in subalpine forests of the Southern Rocky Mountains, USA. Panel (a) gives the relative importance of predictor variables and panels (b–e) display predicted maps and histograms of species-specific live basal areas, restricted by pre-outbreak distributions of each species (USFS, 2021). In (a), greater relative importance indicates the percent contribution of a given variable to overall model accuracy. The modelled relationships between each predictor and response variable are indicated as positive (+), negative (−) or nonlinear (⌒). Note that in (b–e) histograms, bin widths are uneven and *y*-axes are transformed to facilitate comparisons among species. LOS: length of 2019 growing season; SOS: start date of 2019 growing season; EVI2 Amp: 2019 seasonal variation in the enhanced vegetation index (EVI); EVI2 Max: 2019 maximum EVI. Other predictor variable definitions are provided in Table 1.

herbivory in areas with high ungulate populations (Andrus, Hart, & Veblen, 2020; DeRose & Long, 2010) and ungulates can be particularly abundant following bark beetle outbreaks (Ivan et al., 2018). In addition, recent aspen mortality has been widespread due to severe drought, the spread of the invasive scale insect *Lepidosaphes ulmi* (oystershell scale) and a range of fungal pathogens (Anderegg, Flint, et al., 2015; Crouch et al., 2021; Hanna & Kulakowski, 2012; Worrall et al., 2010). These impacts are likely to increase with climate warming and expanding urbanization (Crouch et al., 2021; Kolb et al., 2016; Lukas et al., 2014).

In contrast, we expect that shifts towards subalpine fir dominance will be enhanced by the abundant seedling densities and rapid growth rates of this species that we identified in predictive maps (Figures 5e and 6d). Indeed, persistent increases in the dominance of subalpine fir and other shade-tolerant coniferous species have been noted following drought, blowdown and bark beetle outbreaks throughout the western US (Perovich & Sibold, 2016; Sibold et al., 2007; Veblen et al., 1989; Veblen et al., 1991; Young et al., 2020). These longer-term shifts towards subalpine fir dominance may have critical implications for future ecosystem dynamics. Although recent WBBB outbreaks were of lower severity than outbreaks of MPB and SB in our study area, compositional shifts towards subalpine fir could lead to more severe outbreaks of WBBB in the future because host tree abundance is a key predictor of susceptibility (Harvey et al., 2021). Similarly, increases in subalpine fir dominance may be maladaptive to future warming because this species is more sensitive to drought than other subalpine conifers (Bigler et al., 2007).

4.2 | Region-wide variation in post-outbreak forest conditions

Pre-outbreak forest conditions broadly influenced forest structure and composition following recent bark beetle outbreaks. For example, pre-outbreak species basal area maps were consistently important predictors of post-outbreak live basal areas in our analyses (Figure 4a). Given the relatively slow growth of subalpine conifers in the SRM (Aplet et al., 1988; Chai et al., 2019) and our comparatively short study period (i.e. 23 years), we infer that maps of post-outbreak basal area primarily reflect the survival of large trees that pre-dated recent outbreaks. Other studies demonstrate that variability in

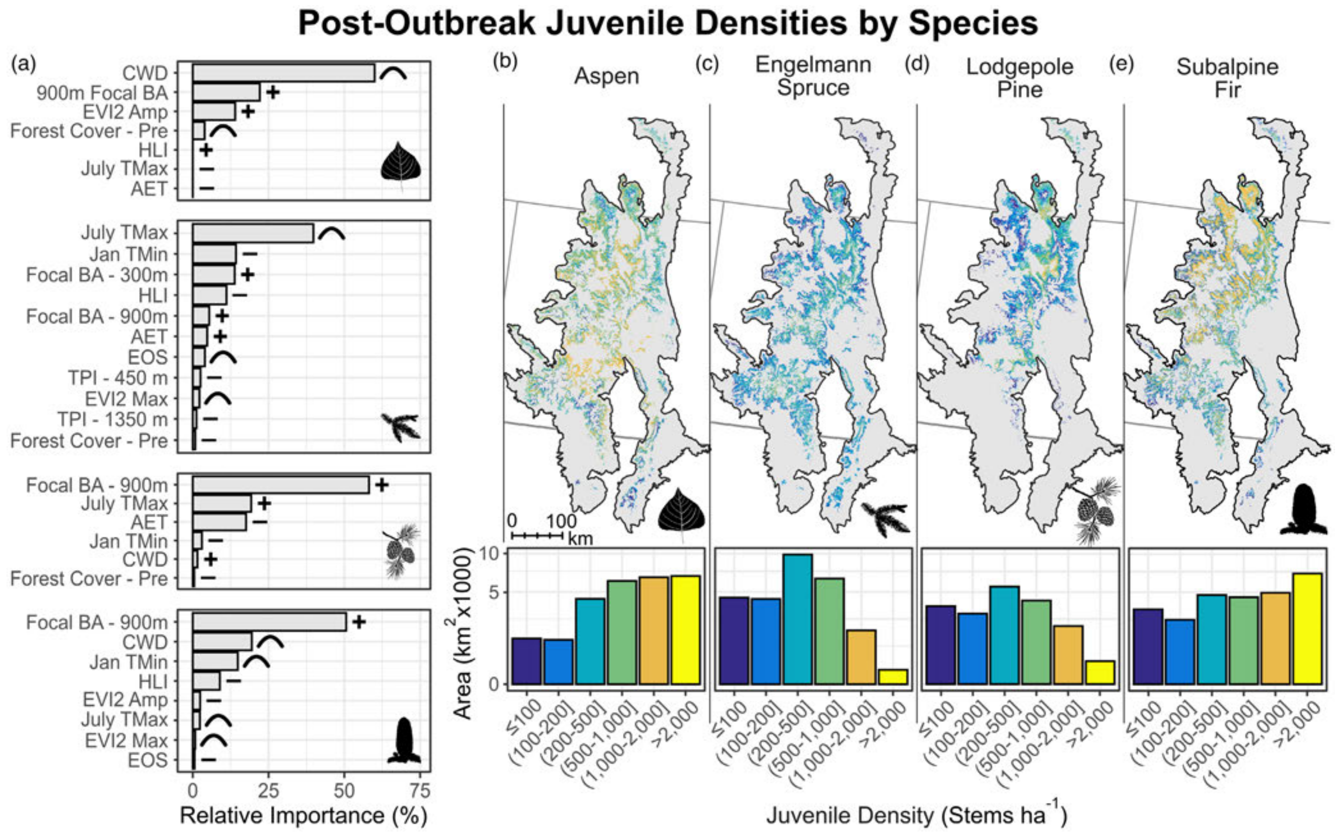

FIGURE 5 Results from generalized linear mixed models of post-outbreak juvenile (<1.4 m in height) densities of four common tree species in subalpine forests of the Southern Rocky Mountains, USA. Panel (a) gives the relative importance of predictor variables and panels (b–e) display predicted maps and histograms of species-specific juvenile densities, restricted to areas within 500 m of the pre-outbreak distributions of each species (USFS, 2021). In (a), greater relative importance indicates the percent contribution of a given variable to overall model accuracy. The modelled relationships between each predictor and response variable are indicated as positive (+), negative (−) or nonlinear (⌒). Note that in (b–e) histograms, bin widths are uneven and *y*-axes are transformed to facilitate comparisons among species. AET: actual evapotranspiration; CWD: climatic water deficit; EOS: end date of 2019 growing season; EVI2 Amp: 2019 seasonal variation in the enhanced vegetation index; EVI2 Max: 2019 maximum enhanced vegetation index; HLI: continuous heat load index. Other predictor variable definitions are provided in Table 1.

pre-outbreak forest conditions relates to past disturbance history (Kulakowski et al., 2012; Rodman et al., 2019; Veblen et al., 1994) and species-specific climatic effects on tree establishment, growth and survival (Andrus et al., 2018; Buechling et al., 2017; Martin & Canham, 2020). Likewise, our models of juvenile density were strongly influenced by pre-outbreak species basal area in the surrounding landscape (Figure 5a). Indeed, tree establishment is often limited by dispersal from adjacent trees of the same species (typically <200 m; McCaughey et al., 1986; Stevens-Rumann & Morgan, 2019) or the location of existing root structures (e.g. aspen re-sprouting). We also found that juvenile densities of aspen, Engelmann spruce and lodgepole pine were highest in areas with low to moderate pre-outbreak forest cover, indicating that localized canopy gaps play a critical role in tree establishment and forest recovery. Such patterns align with known species traits; aspen and lodgepole pine have low shade tolerance and spruce can regenerate well in canopy gaps with bare mineral soil, whereas fir establishes well in closed-canopy forests with thick litter (Burns & Honkala, 1990a, 1990b; Noble & Alexander, 1977). Prior research has also shown that pre-outbreak species basal area and total forest cover influence post-outbreak forest conditions (e.g. Carlson et al., 2020; Pappas et al., 2020; Pettit et al., 2019; Redmond & Kelsey, 2018; Schapira, Stevens-Rumann, Shorrock, Hoffman, & Chambers, 2021). Taken together, our results and those of prior studies indicate that biological legacies and pre-outbreak conditions play a central role in forest trajectories following bark beetle outbreaks.

Outbreak severity has also shaped forest conditions and processes following recent outbreaks in the SRM, with remotely sensed outbreak severity improving our predictions of post-outbreak basal area and height growth rates (Figures 5a and 6a). The severity of recent bark beetle outbreaks has been widely variable throughout the SRM, with stands ranging from low-level mortality (<5% basal area), to a near-total loss of overstory canopy (>90%; Rodman, Andrus, et al., 2021). Indeed, severity had very limited autocorrelation at spatial scales >5 km and patches of near-total canopy loss were small (<0.24 km^2) and isolated (Rodman, Andrus, et al., 2021). Such variability has created heterogeneous forest overstory conditions throughout subalpine

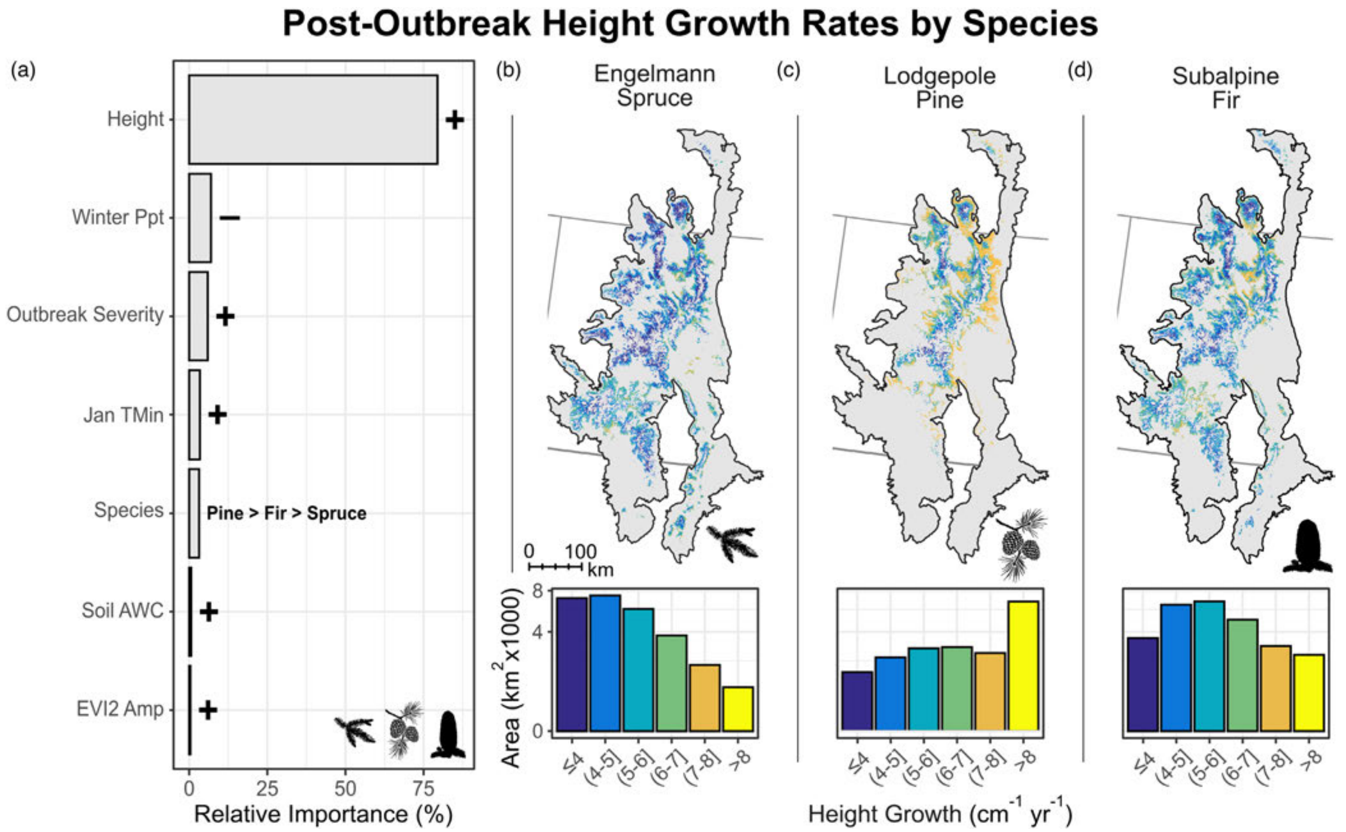

FIGURE 6 Results from the generalized linear mixed model of post-outbreak height growth rates of juveniles (<1.4 m in height) and saplings (≥1.4 and <3 m in height) of three common coniferous tree species in subalpine forests of the Southern Rocky Mountains, USA. Panel (a) gives the relative importance of predictor variables and panels (b-d) display predicted maps and histograms of species-specific height growth rates, restricted to areas within 500 m of the pre-outbreak distributions of each species (USFS, 2021). In (a), greater relative importance indicates the percent contribution of a given variable to overall model accuracy. The modelled relationships between the predictors and response variable are indicated as positive (+), negative (−) or nonlinear (⌒). Note that in (b-d) histograms, *y*-axes are transformed and bin widths are uneven for interpretability. EVI2 Amp: 2019 seasonal variation in the enhanced vegetation index; Soil AWC: soil available water capacity in the top 2 m of the soil column. Other predictor variable definitions are provided in Table 1.

forests of the SRM, a pattern which is further elucidated by our species-specific maps of live basal area. We also found that height growth rates of conifer juveniles were highest in areas with severe outbreaks, a potential compensatory response that is likely to shape future forest dynamics (Figure 6a). Following bark beetle outbreaks, enhanced growth of surviving trees has been identified through tree ring studies of post-outbreak forest dynamics (Jarvis & Kulakowski, 2015; Romme et al., 1986; Veblen et al., 1991) and field sampling across gradients of outbreak severity (Andrus, Hart, & Veblen, 2020; Pelz et al., 2018; Rhoades et al., 2017). However, our region-wide predictive maps of height growth (Figure 6b–d) provide new insight into how such effects on individual organisms can scale up to create heterogeneous processes at the ecosystem level.

Remotely sensed phenology, terrain and climate were important predictors in our models of forest conditions and growth rates, illustrating that species' niches play an instrumental role in post-outbreak forest ecosystem dynamics in our study area. Tree species in the SRM are arranged along such gradients, with lodgepole pine and aspen typically occupying low- to mid-elevation sites in subalpine forests and Engelmann spruce and subalpine fir occupying mid- to high-elevation sites (Peet, 1981; Romme et al., 2009). Our models of live basal area and juvenile density reflect these patterns (Figures 4a and 5a), with aspen and lodgepole pine being most abundant in sites with long growing seasons (*c*. 150 days), early growing season start dates (late May) and high climatic water deficits (>300 mm). In contrast, spruce and fir typically occupied sites with short growing seasons (*c*. 100 days), late growing season start dates (early July), moderate water deficits (200–400 mm) and protected topographic settings. Climatic gradients and their influences on species distributions have been widely studied throughout forests of North America (e.g. Bell et al., 2014; Dobrowski et al., 2015; Rehfeldt et al., 2006). However, the effects of climate and terrain on population vital rates and individual performance are poorly understood. Individual performance is often related to size or other individual-level factors (Bolnick et al., 2011; Clark et al., 2021). Thus, it was not surprising that stem height was the strongest single predictor of height growth rates in our study (Figure 6a). However, after accounting for individual factors, we found that growth was most rapid at subalpine sites with low average winter precipitation

(<500 mm) and high January minimum temperatures (>−13°C), typical of low elevations and warmer areas. These findings were relatively consistent among species, despite interspecific differences in their environmental tolerances. One experimental study with a subset of our study species shows similar results, wherein juveniles had more rapid height growth on warmer, drier sites (Carroll et al., 2021). Primary productivity (e.g. height and radial growth rates) in subalpine forests is often limited by the length of the growing season, which, in turn, is influenced by winter precipitation and temperature (Knowles et al., 2020).

In contrast with our findings concerning juvenile growth, we found that overall juvenile densities were generally greatest at moderate to high elevations (Figure 5). For example, juvenile densities of spruce and pine were highest at sites with low January minimum temperature, and aspen, spruce and fir were most abundant at sites with moderate values of July maximum temperature or annual climatic water deficit (Figure 5a; Figures S4.5–S4.8). Broader ecological theory suggests that vital rates such as growth, reproduction and survival can be negatively correlated at the population level (Laughlin et al., 2020; Sheth & Angert, 2018; Villellas et al., 2015). Indeed, there are inherent trade-offs between traits that confer competitive ability and those that confer tolerance to low-resource environments (McGill et al., 2006), as evidenced by negative relationships between height growth rates and water use efficiency in some conifers (e.g. Dixit et al., 2022). While additional research is needed to understand subalpine tree species performance across abiotic gradients, we infer that low juvenile densities in warm, dry sites could be partially driven by high mortality in such areas (e.g. high fir mortality on dry sites; Carroll et al., 2021). Our finding that climate may have opposing effects on juvenile height growth rates and juvenile densities aligns with broader ecological theory, indicating that individual vital rates (e.g. growth, survival) do not respond consistently to abiotic factors. Thus, increasing temperatures and aridity associated with climate change (Lukas et al., 2014; Pederson et al., 2011) will have important influences on future subalpine forest dynamics that may unfold in complex and unpredictable ways.

4.3 | Study limitations

The field data included in this study were collected opportunistically and were not stratified across the wide range of conditions present throughout the SRM. While we found that these data were representative of conditions across the broader region in most cases, field sampling preferentially targeted forests affected by MPB and SB with >50% basal area mortality. However, areas with low- and moderate-severity outbreaks were still represented; 23.6% of our field plots were in areas with less than 50% basal area mortality and 4.6% of our plots were in areas with less than 10% basal area mortality. In addition, we used spatial data layers to infer post-outbreak forest conditions across unsampled areas throughout the SRM, which span a wide range of outbreak severities (Figure 1). The various field studies included here also had a range of plot sizes and sampling protocols, and this variability may have influenced our results. However, we standardized datasets and used mixed-effects models to help account for these differences. We obtained maps of pre-outbreak species basal area and canopy cover from available sources, and these data did not perfectly align with the beginning of the study period (i.e. 2000–2002 vs. 1997). Because the vast majority of bark beetle-caused tree mortality in the study period occurred after 2002 (Chapman et al., 2012; Hart et al., 2017; Harvey et al., 2021; USFS, 2020), we assumed that these spatial datasets effectively captured pre-outbreak forest conditions despite missing the first 3 to 5 years of the study period. Lastly, we did not assess the effects of management, wildfire or climate change on forest dynamics throughout beetle-affected forests of the SRM. Although these questions were beyond the scope of this study, they represent a fruitful area for future research.

5 | CONCLUSIONS

Here we show that beetle-affected subalpine forests of the SRM are likely to remain forested through the survival of mature non-host trees, high densities of advance regeneration and the rapid post-outbreak growth of saplings and juveniles. Our analyses using field data and regional geospatial modelling suggest that most stands will eventually recover to pre-outbreak densities in the absence of other disturbances. In contrast, shifts in forest composition, particularly towards subalpine fir, are likely to endure for decades. This research highlights the value of integrating (1) widespread field surveys, (2) satellite-based remote sensing data, (3) ancillary GIS data and (4) aerial detection survey data to make broader inferences than can be gained from any single data source. By using these disparate datasets in complementary analytical approaches, we demonstrated the variable effects of bark beetle outbreaks on forest conditions throughout a complex region. The capacity of systems to cope with disturbance may be enhanced through structural, compositional and spatial heterogeneity (Angeler & Allen, 2016; Elmqvist et al., 2003; Turner, 2010); thus, the variable responses to beetle outbreaks across the SRM region – driven by patterns of pre-outbreak conditions, outbreak severity and species-specific environmental tolerances – are likely to contribute to persistent ecosystem functioning despite future disturbance. While recent outbreaks of native bark beetles have been widespread, causing tree mortality across millions of hectares throughout western North America (Bentz et al., 2009; Raffa et al., 2008), these outbreaks are not catastrophic disturbances driving forest loss (Rocca & Romme, 2009). However, shifts in size structure and species composition have the potential to influence ecosystem services, susceptibility to subsequent disturbances and future forest dynamics. Region-wide analyses such as those presented here provide critical insight into the ecological effects of recent disturbances, as well as the way that these effects vary across broad forested landscapes.

AUTHOR CONTRIBUTIONS

Conceptualization, Kyle C. Rodman and Sarah J. Hart; Methodology, Kyle C. Rodman and Sarah J. Hart; Software, Kyle C. Rodman; Validation, Kyle C. Rodman; Formal Analysis, Kyle C. Rodman; Investigation, Kyle C. Rodman, Robert A. Andrus, Amanda R. Carlson, Trevor A. Carter, Teresa B. Chapman, Jonathan D. Coop, Paula J. Fornwalt, Nathan S. Gill, Brian J. Harvey, Katharine C. Kelsey, Jenna E. Morris, José F. Negrón, Katherine M. Nigro, Gregory S. Pappas, Miranda D. Redmond, Charles C. Rhoades, Zoe H. Schapira, Thomas T. Veblen and Jianmin Wang; Resources, Sarah J. Hart; Data Curation, Kyle C. Rodman, Robert A. Andrus, Amanda R. Carlson, Trevor A. Carter, Teresa B. Chapman, Jonathan D. Coop, Paula J. Fornwalt, Nathan S. Gill, Brian J. Harvey, Katharine C. Kelsey, Daniel C. Laughlin, Jenna E. Morris, José F. Negrón, Katherine M. Nigro, Gregory S. Pappas, Miranda D. Redmond, Charles C. Rhoades, Zoe H. Schapira, Thomas T. Veblen and Jianmin Wang; Writing—Original Draft Preparation, Kyle C. Rodman; Writing—Review & Editing, All authors; Visualization, Kyle C. Rodman; Supervision, Kyle C. Rodman and Sarah J. Hart; Project Administration, Kyle C. Rodman and Sarah J. Hart; Funding Acquisition, Brian J. Harvey, Thomas T. Veblen, Sarah J. Hart All authors have read and agreed to the submitted version of the manuscript.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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DATA AVAILABILITY STATEMENT

Processed data, statistical models, regional maps and R code used in this project are available through Dryad Digital Repository https://doi.org/10.5061/dryad.7sqv9s4sh (Rodman et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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