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RESEARCH ARTICLE

Understory plant community responses to widespread spruce mortality in a subalpine forest

Trevor A. Carter[1] | Paula J. Fornwalt[2] | Kathleen A. Dwire[2] | Daniel C. Laughlin[3]

[1]Department of Integrative Biology, University of Colorado Denver, Denver, Colorado, USA

[2]US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA

[3]Botany Department, University of Wyoming, Laramie, Wyoming, USA

Correspondence
Trevor A. Carter, Department of Integrative Biology, University of Colorado Denver, 1201 Larimer Street, Denver, CO 80203.
Email: trevor.carter@ucdenver.edu

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Abstract

Aims: Spruce beetles (*Dendroctonus rufipennis*) are causing widespread spruce (*Picea* spp.) mortality in subalpine forests in western North America. Spruce beetles are changing forest structure and composition by killing a dominant overstory species, but we know little about how the understory community responds to the increase in resource availability brought about by spruce mortality, what mechanisms drive its response, or how its response affects other forest properties and processes.

Location: Glacier Lakes Ecosystem Experiments Site, Medicine Bow Mountains, Wyoming, USA.

Methods: We measured understory community cover and richness in 75 permanent plots during and 10 years after an epidemic spruce beetle outbreak, and measured trait values for 46 common understory species. We used linear regression to determine how the understory community has changed over time and along a gradient of spruce mortality, and to evaluate the relative support for two mechanisms contributing to species responses.

Results: Understory cover nearly doubled between sampling periods and increased the most where spruce mortality was most severe. Understory richness doubled and showed a weak positive trend with spruce mortality. Understory species with the largest increases in cover were the most frequent across the landscape before the disturbance, were the tallest at maturity and had the lowest leaf turgor loss points. Fir seedling density decreased over time, with decreases lessening with increases in understory cover. Changes in spruce seedling density were not predicted by changes in understory cover.

Conclusions: Our findings highlight some of the diverse ways in which understory communities can be altered by spruce beetle outbreaks, and how the direction and magnitude of change can depend on the amount of spruce mortality as well as on priority effects and traits of pre-disturbance species. Our findings also highlight how understory community changes can have implications for other forest properties and processes, such as tree regeneration and forest recovery.

KEYWORDS
disturbance, Engelmann spruce (*Picea engelmannii*), functional traits, priority effects, spruce beetle, spruce–fir forest, subalpine forest, understory community assembly

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1 | INTRODUCTION

Disturbances shape the structure and composition of vegetation (Oliver, 1980; Bazzaz, 1983; Harvey et al., 2016; Seidl et al., 2016), but these effects differ among disturbance agents and the ecosystems in which they occur (Pickett & White, 1985; Walker, 1999). Insect outbreaks at large are a global disturbance capable of disrupting forest landscapes and have been increasing as climates change (Seidl et al., 2017). Bark beetles in the genus *Dendroctonus* are a primary agent of forest disturbance in western North American coniferous forests (Baker & Veblen, 1990; Veblen et al., 1991; Diskin et al., 2011; Derderian et al., 2016; Audley et al., 2020). In the early 2000s, spruce beetle (*Dendroctonus rufipennis*) activity increased significantly in western North American subalpine forests (Hart et al., 2015; Frank et al., 2019; Pettit et al., 2019), causing landscape-scale tree mortality covering millions of hectares (Raffa et al., 2008). Spruce beetles preferentially attack spruce (*Picea* spp.) trees and in combination with their fungal associates are the most significant agent of mortality for mature *Picea* (Holsten et al., 1999). Similar to other large natural disturbances in subalpine forests such as fire, windthrow, and outbreaks of other forest insects, spruce beetles create heterogeneous patches of tree mortality across the landscape (Derose & Long, 2010).

Although the effects of spruce beetle outbreaks on subalpine forest overstory structure and composition have been documented across western North America (Veblen et al., 1991; Derderian et al., 2016), the effects on understory plant communities have received little attention (but see Davis et al. 2020). The response of understory plants to spruce beetle disturbance in subalpine forests is particularly important for ecosystem functions such as carbon sequestration, wildlife habitat, and forest regeneration. First, gross primary production of understory plant communities can reach up to 39% of total canopy gross primary production (Misson et al., 2007). Insect disturbances have been shown to strongly reduce the net atmospheric CO_2 exchange in forested systems (Clark et al., 2010). Yet despite 85% canopy mortality by spruce beetles in a Rocky Mountain subalpine forest, the atmospheric fluxes of CO_2 and H_2O remained relatively constant (Speckman et al., 2015). This resilience in carbon sequestration may have been influenced by an increase in understory leaf area, which can be a significant factor in net ecosystem gas exchange (Misson et al., 2007). Second, pollinator and avian community diversity has been shown to be higher following bark beetle disturbance events because of increases in species richness and increased heterogeneity in forest structure (Rhoades et al., 2018; Przepióra et al., 2020). Third, Engelmann spruce (*Picea engelmannii*) regeneration 20 years after an epidemic spruce beetle outbreak was positively associated with increases in the percent cover of understory plants (Pettit et al., 2019). This suggests that understory responses can moderate the potential negative effects created by opening of the forest canopy and the rapid change in the light environment that may not favor shade-tolerant tree species, like *P. engelmannii* and subalpine fir (*Abies lasiocarpa*; Alexander & Shepperd, 1984; Velasco & Mattsson, 2020). The regeneration of these forests to pre-disturbance conditions is uncertain because changing climatic conditions may not promote *Picea* regeneration (Kueppers et al., 2017).

Understory plant communities may ultimately benefit from increases in light and other resources brought about by tree mortality (Barbier et al., 2008). Understory plant communities, particularly annual and biennial forbs and graminoids, have been shown to increase in productivity and diversity following fire (Laughlin & Fulé, 2008; Romme et al., 2016), mountain pine beetle (*Dendroctonus ponderosae*) outbreaks (Pappas et al., 2020; Runyon et al., 2020; Pec et al., 2015), western balsam bark beetle (*Dryocoetes confusus*) outbreaks (McMillin et al., 2003), and spruce budworm (*Choristoneura fumiferana*) outbreaks (Kemball et al., 2005). However, it is unclear whether, or to what extent, the understory plant community will respond to spruce beetle disturbance. In addition, it is not known whether these responses will be analogous to the responses following other large natural disturbances, what effects the understory plant community has on tree seedling densities within the context of spruce beetle disturbances (Pettit et al., 2019), or what mechanisms regulate the understory response to this widespread canopy mortality.

Two potential, but not mutually exclusive, mechanisms that could explain understory plant responses to this disturbance agent are priority effects and species adaptations reflected in their functional traits. On the one hand, if priority effects are at play, plant species that were the most frequent across the forested landscape prior to disturbance may have priority and exhibit the largest response given that the understory was not directly disturbed (Turner et al., 1998). These species are already well-established and may therefore be able to outcompete species that were uncommon or absent prior to the disturbance (Symons & Arnott, 2014). The intact understory plant community has its own inertia and these priority effects can strongly influence the patterns of community assembly following disturbance (Turner et al., 1998; Stevens et al., 2019).

By contrast, understory plant species that are adapted to respond to increases in resource availability (Jentsch & White, 2019) might exhibit the largest response to the disturbance (Keddy, 1992; Violle et al., 2007). Taller species may suppress the growth of shorter species because they can intercept more of the available light coming through the canopy (Canham et al., 1990; Navas & Violle, 2009). Species with acquisitive leaf traits, such as high specific leaf area and low leaf dry matter content, may exhibit faster growth than species with conservative leaf traits (Wright et al., 2004; Laughlin et al., 2010). This may be in part because species with acquisitive leaf traits can better uptake nitrogen made available due to tree mortality (Speckman et al., 2015; Boggs Lynch et al., 2021). Subalpine forests are not normally water limited and precipitation may occur in any month of the year (Regan et al., 1998). Species that invest resources into drought tolerance instead of growth may be outcompeted by less drought-tolerant neighbors. As such, we expected species that were the least tolerant of drought (i.e., species with higher turgor loss points) to exhibit the fastest responses to an increase in resource availability. Lastly, because dispersal limitation is a key constraint in community assembly (Laughlin et al., 2020b; Gill et al.,

2021), species with mechanisms that allow for widespread dispersal, such as wind-driven dispersal, may increase in abundance following disturbance. Priority effects and functional traits are not mutually exclusive, and both may influence the understory community response to disturbance.

To fill these gaps in our understanding of understory plant responses to *Picea* mortality, and the implications of these responses, we quantified the understory response to a spruce beetle epidemic in a subalpine *P. engelmannii–A. lasiocarpa* forest in the Medicine Bow Mountains of southeast Wyoming, USA (Figure 1a). Our research objectives were three-fold: (1) quantify how understory plant community cover and richness have changed since the disturbance and along environmental gradients; (2) assess the influence of understory cover changes on tree seedling density changes; and (3) evaluate the relative support for priority effects and functional traits as predictors for species' responses to disturbance. First, we predicted that the understory community in this *Picea–Abies* forest would have increased in total cover and species richness in response to increases in resource availability following *Picea* mortality, with greater increases occurring in areas of greater mortality (McMillin et al., 2003; Laughlin & Fulé, 2008; Edwards et al., 2015; Pec et al., 2015). We predicted greater increases in species cover and richness in stands that are at lower elevations and on more southerly aspects because these environments are not only more favorable habitat for spruce beetles (Coulson, 1979), but have longer growing seasons for understory plants to establish and grow. Second, we predicted that changes in seedling densities for the two dominant overstory tree species, but especially *P. engelmannii*, would be positively related to changes in understory cover because of the potential facilitation by understory

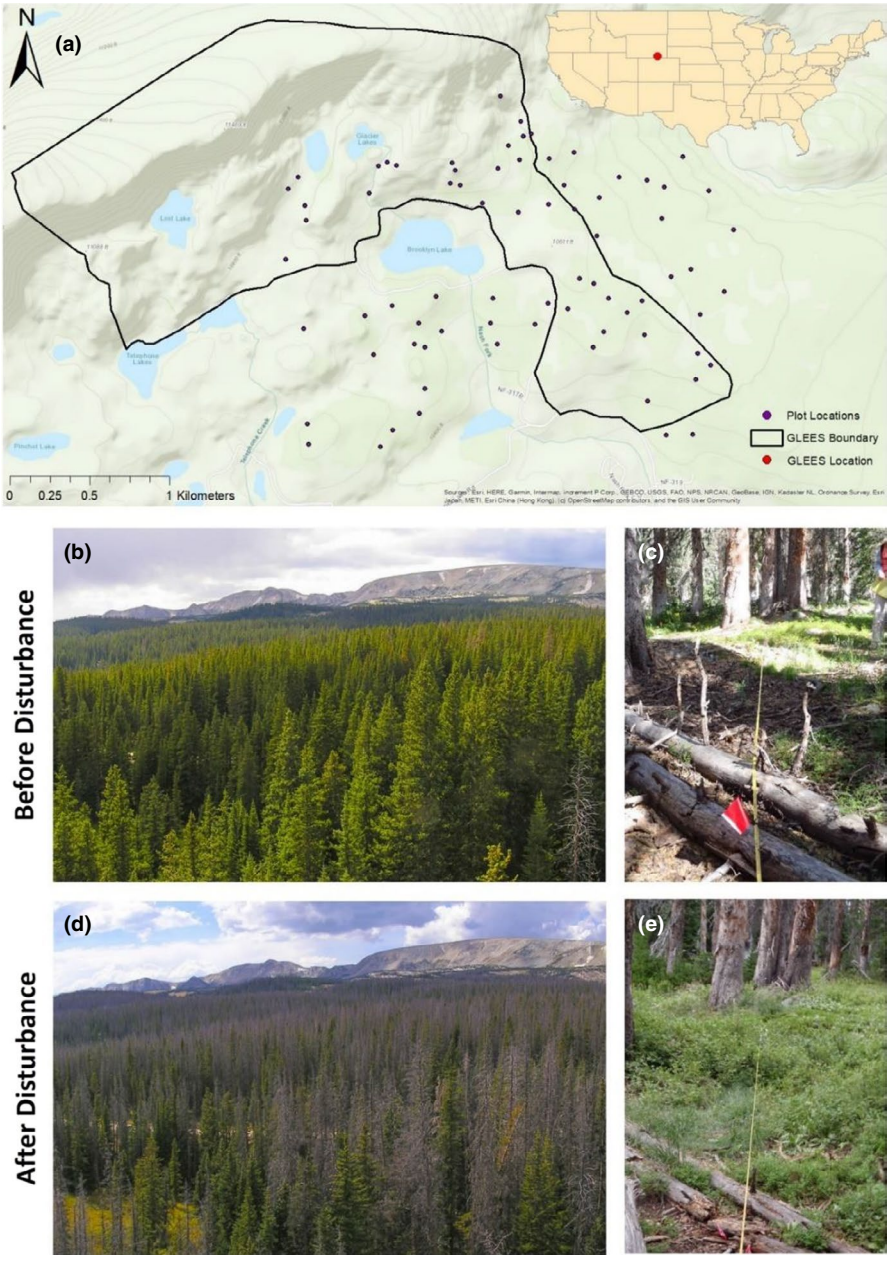

FIGURE 1 (a) Map of study area, the Glacier Lakes Ecosystem Experiments Site (GLEES), located in southeastern Wyoming within the context of the United States. Repeat photography before the disturbance (b, c) and 10 years after the disturbance (d, e). Photos of the overstory (b, d) were provided by Dr John Frank. Photos of the understory (c, e) are from a plot that experienced high (100%) overstory mortality

species (Pettit et al., 2019). Third, we predicted species that were more frequent across the forested landscape prior to disturbance (Keddy, 1992; Turner et al., 1998), and species with traits associated with rapid resource acquisition, such as taller stature, higher specific leaf area, lower leaf dry matter content, higher turgor loss point, and species with wind-dispersed seeds would increase more than those without such traits (Canham et al., 1990; Westoby et al., 2002; Wright et al., 2004; Violle et al., 2007; Navas & Violle, 2009; Laughlin et al., 2010, 2020a, 2020b; Gill et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted within and adjacent to the Glacier Lakes Ecosystem Experiments Site (GLEES; Musselman, 1994; Figure 1a). GLEES is a 600 ha experimental area located within the Medicine Bow Mountains of the Medicine Bow National Forest, and is approximately 55 km west of Laramie, Wyoming, USA at 41°22′30″N and 106°15′30″W. Soils are formed from a quartzite bedrock and are generally shallow (Musselman, 1994). The elevation of GLEES ranges from 3,200 to 3,500 m. Minimum and maximum average hourly temperatures range from −23°C to −1°C in the winter months and from −7°C to 21°C in the summer months. Precipitation is possible in any month with an average of 125 cm annually, but predominantly falls as snow with a mean maximum snowpack depth of 2 m (Musselman, 1994). The dominant plant communities at GLEES are wet and dry subalpine meadows, wet and dry subalpine forests, wet and dry krummholz forests, and wet and dry alpine meadows (Regan et al., 1998).

A spruce beetle epidemic occurred in the subalpine forests at GLEES from the mid to late 2000s to the early 2010s (Frank et al., 2014). Beetle attacks on overstory *P. engelmannii* peaked in 2008 (Frank et al., 2014). However, *P. engelmannii* often have a 1–3-year delay between attack, mortality and needle cast, and so a concomitant peak reduction in overstory tree leaf area index due to needle cast did not occur until about 2010 (Mast & Veblen, 1994; Frank et al., 2014).

2.2 | Forest plot sampling

We first sampled forest vegetation across 75 randomly distributed, permanently marked, fixed-radius plots (0.01 ha) in 2010–2012 (hereafter referred to as 2010). Of the 75 plots, 37 had originally been established and sampled in 1989–1991 (hereafter 1989) to characterize the diverse assemblage of plant communities at GLEES (Regan et al., 1998). The locations of plots in the 1989 plot network had been determined using a 100 m × 100 m grid placed over a map of GLEES, with one plot randomly located per grid cell. We deemed the 37 plots suitable for inclusion in our study because they could be relocated in the field, contained 10 or more *P. engelmannii* and/or *A. lasiocarpa* trees with a non-krummholz growth form, and had minimal human disturbance. We established the remaining 38 plots in 2010 to better evaluate the impact of spruce beetles by expanding the study area. To locate these additional plots, we first delineated a 5.6 km^2 area in and around the beetle-impacted forested portion of GLEES using ArcGIS (ESRI 2020. ArcGIS Desktop: Release 10.8.1. Redlands, CA: Environmental Systems Research Institute). We then imposed 200 m × 200 m grid cells over the area and if a grid cell did not already contain at least one plot from the 1989 network, we placed a random point in it to serve as the center of a potential new plot. We then visited each cell to locate potential plot locations, and established 38 plots because they met the criteria used to establish the original plots.

We re-sampled the 75 plots 10 years after the disturbance in 2019–2020 (hereafter 2020), to compare with the pre-disturbance forest conditions (Figure 1c,e). Only one plot near a road was sampled in 2019 prior to roadside hazard tree removal; the remaining 74 plots were sampled in 2020. In 2020 we relocated plots using GPS coordinates recorded at the plot center in 2010. Plots falling within the beetle grid were located using a handheld GPS unit. Three sampling transects 5.64 m in length were established in each suitable plot. Transects extended from the plot center to the perimeter of the plot. Transect azimuths for old plots were the same as those that had been established previously, whereas the azimuths for new plot transects were determined using random number tables. Transects of new plots had to be at least 20° apart.

In both the 2010 and 2020 sampling periods, we sampled understory forbs, shrubs, and graminoids in five evenly spaced Daubenmire quadrats (20 cm × 50 cm) along each of the three 5.64 m transects that radiated out from plot center. We measured cover of each understory plant species to the nearest percent in each quadrat. Species cover estimates were averaged per transect and then per plot. For each plot, understory species richness was also assessed by listing all species found in the Daubenmire quadrats as well as during an approximate 10-min walk through the plot. Each species sampled (Appendix S1) was assigned a growth form (forb, shrub, or graminoid) based on the local flora (Dorn & Dorn, 2015).

In 2010 we recorded the diameter at breast height and species of all overstory trees within the plot and we tagged them. We defined overstory trees as individuals >137 cm tall (Regan et al., 1998). To compare live tree basal area (hereafter referred to as basal area) before and after the disturbance, we also assigned crown conditions to all trees sampled. We considered a tree alive if it had any green foliage and noted any signs of recent beetle attack (e.g., pitching, frass), or if the tree's foliage had begun to discolor or drop. We considered a tree dead if it had no green foliage; we also noted if its mortality was likely due to beetles or if other causes of mortality (i.e., competitive exclusion) were likely. The difference in basal area before and after the disturbance was calculated to assess the canopy mortality in each plot. Significant changes in canopy mortality were driven by the reduction in *Picea* basal area (paired *t* mean difference in *Picea* basal area 20.81 m^2/ha, $p < 0.001$); *Abies* experienced a non-significant decrease in basal area (paired *t* mean difference in *Abies*

basal area −1.11 m^2/ha, $p = 0.210$). Post-disturbance overstory sampling in 2020 focused on both re-measuring trees that were sampled and tagged in 2010, as well as measuring and tagging trees that had grown into the plot.

Tree seedlings between 10 and 44 cm tall that were not included in understory cover estimates, were counted by species in every plot in both 2010 and 2020. We selected this size class to maximize accuracy because there is a low probability of receiving an accurate count for seedlings under 10 cm across both sampling periods. In addition, we determined that an upper limit of 44 cm was appropriate because we only had a few understory species that reached this height (Appendix S1) and seedlings taller than 44 cm were less likely to be influenced by understory cover.

We used a convex spherical densiometer to estimate canopy cover within each plot. We recorded four estimates taken from the plot center and facing the four cardinal directions and averaged the values to estimate canopy cover for each plot. Canopy cover measurements were collected both before (2010) and 10 years after (2020) the disturbance. We measured other biologically relevant covariates; in brief, we recorded the elevation of each plot (m) and the aspect, which was then transformed to represent the degrees away from south (|aspect − 180|) (Carlson et al., 2017). In addition, we collected soil moisture and temperature measurements on 60 of the 75 plots at three different times during the 2020 growing season. A full description of the environmental covariates is outlined in Appendix S2.

2.3 | Functional trait sampling

In 2020, leaf samples from five replicate individuals for each of 46 common understory plant species were harvested within the GLEES study area to measure leaf functional traits related to resource acquisition (e.g., light and nutrients) and drought tolerance (Appendix S1). For species with compound leaves or small leaves, samples also included the stem for ease of rehydration. We selected the 46 species, of which 43 were herbaceous and three were shrubs (Appendix S1), because collectively they accounted for 82% of understory species occurrences and 95% of understory cover across all plots before disturbance. Leaf samples were wrapped in a wet paper towel and placed inside a cool and dark cooler for transport to the laboratory within 8 hr of harvest. To rehydrate the leaves the nadir of each sample (e.g., the petiole, non-photosynthetic base of the leaf for plants with basal rosettes, or stem depending on the leaf anatomy) was cut while submerged (Garnier et al., 2001) to prevent embolisms from occurring within the stem that would prevent rehydration. Leaves were rehydrated to full turgor in a refrigerator for 24 hr.

Rehydrated leaves at full turgor were used to measure specific leaf area (cm^2/g; Garnier et al., 2001) and leaf dry matter content (dry mass g/wet mass g; Garnier et al., 2001). Rehydrated leaves were frozen to estimate leaf turgor loss point (MPa; Bartlett et al., 2012a, 2012b) using a vapor pressure osmometer. Frozen leaf samples were cut into four 1-mm^2 squares and placed in the four corners of the vapor pressure osmometer chamber. Measurements of osmolarity were recorded every 90 s until samples reached equilibrium in the chamber. Measurements were then converted into leaf turgor loss point (Griffin-Nolan et al., 2019) using linear models developed for forbs, graminoids, or woody species (Bartlett et al., 2012a; Griffin-Nolan et al., 2019).

Plant height was measured to the nearest centimeter on five mature individuals prior to the harvest of leaf samples for each of the 46 species in the field. Plant height was measured at the tallest point of the plant without moving or altering the plant. We were unable to collect seed mass data for our 46 species. To include a dispersal-related trait, we assigned a dispersal syndrome as a categorical variable (either wind dispersal, dehiscence, endozoochory, or ectozoochory) for each of the 46 species using the fruit morphology presented in the flora of the region and our knowledge of the species (Dorn & Dorn, 2015). For example, species with fleshy berries were categorized as endozoochory, whereas aster species with large well-developed pappi were categorized as wind dispersal.

2.4 | Data analysis and model selection

2.4.1 | Contrasting 1989 and 2010 understory data

A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2014) from the *vegan* package version 2.5-7 (R Core Team, R Foundation for Statistical Computing, Vienna, AT, Oksanen et al., 2020) conducted on the understory community data from the 37 original plots in the 1989 plot network showed that understory community composition was not significantly related to the amount of overstory mortality between the 1989 and 2010 sampling periods (Appendix S3). This suggests that any mortality-related changes in the understory growing environment that may have occurred prior to the 2010 sampling period did not result in a detectable understory response. Therefore, we used understory data from the 2010 sampling period as representative of pre-beetle disturbance conditions (Figure 1b,c).

2.4.2 | Hypothesis 1

To test our hypothesis that understory cover and richness changed in response to the spruce beetle outbreak, we utilized paired *t*-tests for differences from zero for a single distribution of differences and calculated three response variables using pre- and post-disturbance data. For each plot, we calculated the change in total understory cover (cover in 2020 − cover in 2010), the change in total species richness (species richness in 2020 − species richness in 2010), and a Bray–Curtis dissimilarity value, or the similarity in community composition between sampling periods (Beals, 1984). We used a Bray–Curtis dissimilarity value to represent the multivariate response of species to evaluate the potential for emergent trends that may not be detected by using the univariate response of either cover or

richness. We used generalized linear regression to model all of our responses and used a Gaussian error structure to model the change in understory cover and Bray–Curtis dissimilarity values because all assumptions of a Gaussian error structure were met, and the residuals were not over-dispersed. To model the change in species richness we used the same modeling approach but with a quasi-Poisson distribution because the residuals were over-dispersed. For all models, we started with a global model including *Picea* mortality as the predictor as well as other biologically relevant covariates (Appendix S2). We used the dredge function (MuMIn version 1.43.17; Therneau, 2020) to identify the model with the lowest Akaike information criterion (AIC) value (Bolker et al., 2009). We consistently selected the most parsimonious model based on AIC model selection where the delta AIC threshold was greater than two (Bolker et al., 2009). Changes in understory community composition before and after the disturbance represented as Bray–Curtis dissimilarity was further examined using Non-metric Multidimensional (Distance) Scaling (NMDS, 1987) using the metaMDS function in the *vegan* R package (R Core Team, R Foundation for Statistical Computing, Vienna, AT, Oksanen et al., 2020).

In addition to evaluating the change in understory cover and species richness, we used measurements of plot understory cover and species richness before and after the disturbance to examine the trajectories of these response variables in both sampling periods as a function of comparable predictor variables used within the change through time models. Model selection was consistent with the methods used to select the change through time models.

2.4.3 | Hypothesis 2

To test our hypothesis that seedling densities of *P. engelmannii* and *A. lasiocarpa* changed through time, and are positively related to understory cover, we compared seedling densities before and after the disturbance using a paired *t*-test and modeled the change in seedling density (seedlings in 2020 – seedlings in 2010) as a function of the change in understory cover and the change in canopy cover using a Gaussian error structure. We used a Gaussian error structure because a Poisson error structure would not allow for decreases (negative values) in seedling densities.

In addition, to examine the trajectories of seedling densities, we used plot-level seedling counts before and after the disturbance as functions of understory cover and canopy cover in both sampling periods. We used a quasi-Poisson distribution for these models to account for over-dispersed data.

2.4.4 | Hypothesis 3

To test whether priority effects, functional traits, or both predict the change in species-specific cover (cover in 2020 – cover in 2010), we created a linear model that included both species traits and the species pre-disturbance frequency across all plots as predictor variables with the change in species-specific cover as the response variable. The change in species-specific cover was log-transformed so model residuals would be normally distributed. Pre-disturbance frequency was calculated as the number of plots in which the species occurred before the disturbance divided by the total number of plots ($N = 75$). This model used a Gaussian error structure and was compared with similar models in which the dredge function (MuMIn; Therneau, 2020) was used to identify the most parsimonious model using AIC model selection (as above in Hypothesis 1). We compared the final model with models that included traits only, and pre-disturbance frequency only.

We performed all data analysis in R version 3.6.2 (R Core Team, R Foundation for Statistical Computing, Vienna, AT, R Core Team, 2019). We checked all covariates for collinearity and removed collinear covariates accordingly using a corvif function from Zuur et al. (2009). We checked the residuals of the spatially explicit models (all models except for those addressed in Hypothesis 3) for spatial autocorrelation using a Moran's *I* test. Only the Bray–Curtis dissimilarity model showed spatial autocorrelation; for this model, a spatial auto-covariate was calculated and added into the original model statement, which removed the effects of spatial autocorrelation (Dormann et al., 2007).

3 | RESULTS

3.1 | Understory community responses

Across all plots, average understory cover increased significantly ($p < 0.001$ for the differences of the means from the paired *t*-test; 16% ± 4%) following the disturbance (Figure 2a; 25% before vs 41% after disturbance). The change in understory cover was highest where the canopy mortality was greatest, at lower elevations, and on south-facing slopes (Figure 2; Appendix S4). Specifically, the change in understory cover was negatively related to the change in basal area ($p = 0.019$; Figure 2b). Plots at lower elevations exhibited the largest increases in understory cover ($p < 0.001$; Figure 2c), with plots at mid to high elevations exhibiting high variability. The change in understory cover was negatively related to aspect ($p = 0.011$; Figure 2d), such that plots located on south-facing slopes exhibited larger increases in understory cover. The trajectories (i.e., direction of response) of understory cover both before and after the disturbance were largely similar (Appendix S5), except that understory cover was predicted by elevation before the disturbance but not after the disturbance (Appendix S5b).

Average understory species richness doubled (Figure 3a; 9 species per 0.01 ha before vs 18 species per 0.01 ha after disturbance) and this difference was highly significant ($p < 0.001$; 10 ± 1 species). Elevation and aspect were important predictors of the change in species richness (Figure 3; Appendix S6). The change in species richness was negatively related to elevation ($p < 0.001$; Figure 3c). Plots on south-facing aspects had the largest increases in species richness

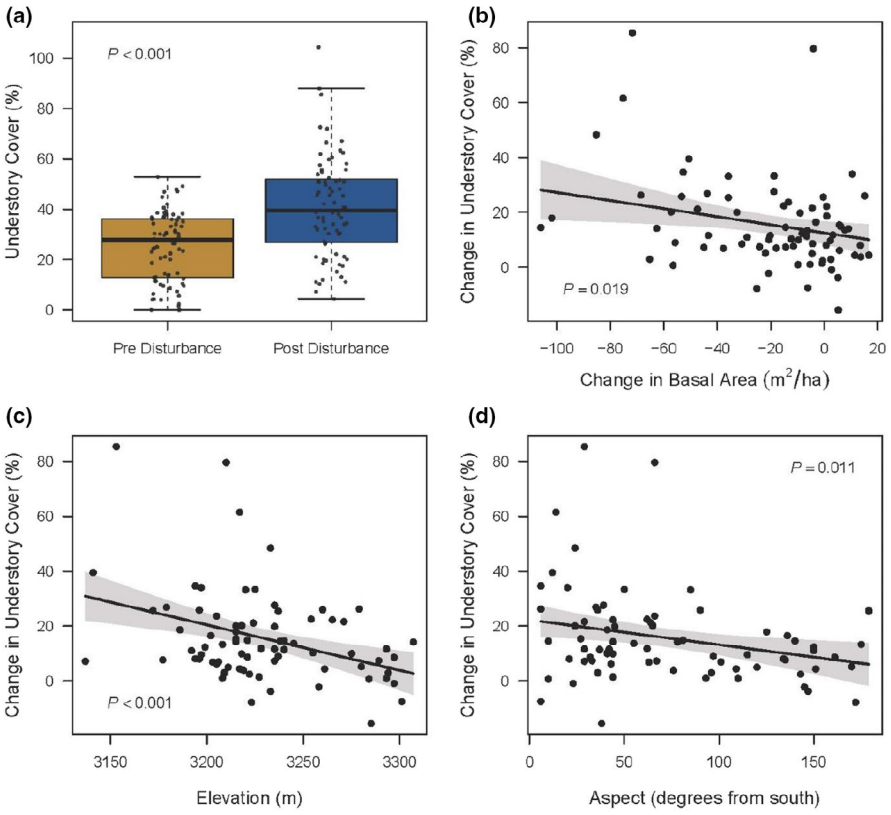

FIGURE 2 Understory cover before and after the disturbance (a), and in response to disturbance as a function of the partial effects of change in basal area (b), elevation (c) and aspect (d). Shaded areas represent 95% confidence intervals. The model using the partial effects of all predictors had an $R^2 = 0.30$ (Summary of model results are in Appendix s4, observed vs predicted plot of model statements are found in Appendix S15c)

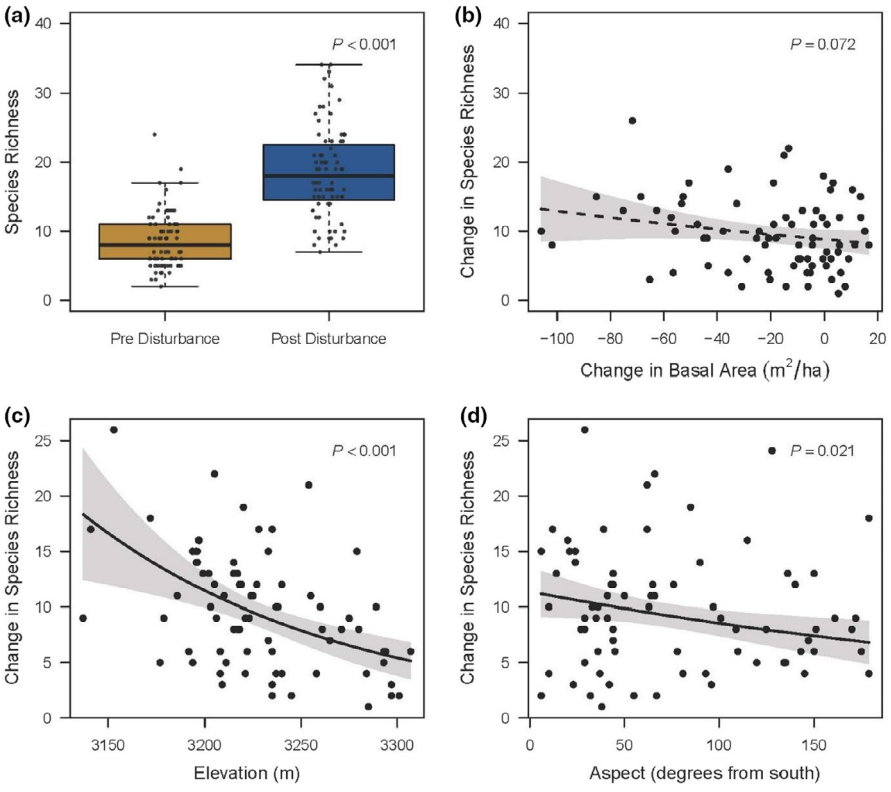

FIGURE 3 Understory species richness before and after the disturbance (a), and in response to disturbance as a function of change in basal area (b), elevation (c) and aspect (d). Shaded areas represent 95% confidence intervals. The model using the partial effects of elevation and aspect had an $R^2 = 0.29$. The dashed line (b) represents a non-significant trend (Summary of model results are in Appendix S6, observed vs predicted plot of model statements are found in Appendix S15f)

($p = 0.021$; Figure 3d). The change in species richness was not significantly related to the change in basal area (Figure 3b), although a weak negative relationship was detected ($p = 0.072$). The trajectories of species richness both before and after the disturbance differed slightly between sampling periods (Appendix S7). Species richness was more strongly predicted by basal area and aspect before the disturbance and by elevation and aspect after the disturbance (Appendix S7).

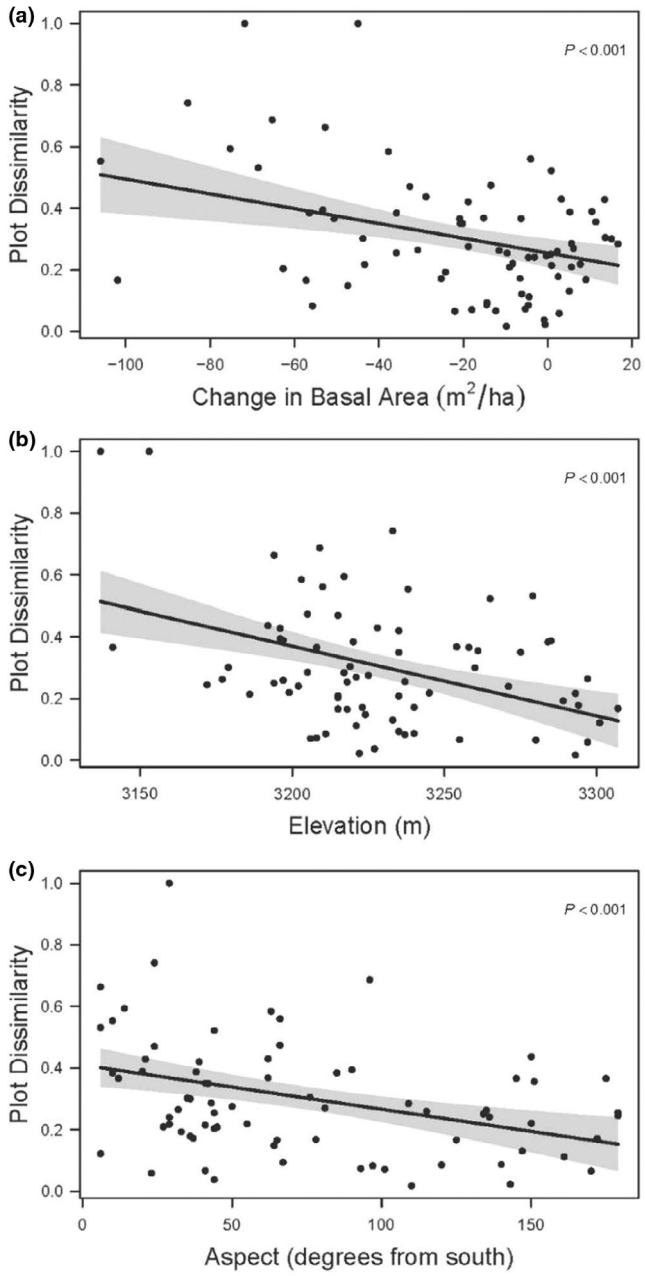

FIGURE 4 Change in community composition (plot level Bray–Curtis dissimilarity between sampling periods) as a function of the partial effects of change in basal area (a), elevation (b) and aspect (c). Shaded areas represent 95% confidence intervals. Each panel depicts a significant predictor used in the final model. The final model had an $R^2 = 0.42$ (Summary of model results are in Appendix S8, observed vs predicted plot of model statements are found in Appendix S15g)

Compositional dissimilarity of the understory between the pre- and post-disturbance sampling periods was negatively related to the change in basal area, elevation, and aspect (Figure 4; Appendix S8). Plots with larger decreases in basal area were less similar in composition after the disturbance relative to pre-disturbance conditions than plots with little or no change in basal area (Figure 4a; $p < 0.001$). Plots at lower elevations had higher dissimilarity than those at higher elevations (Figure 4b; $p < 0.001$), and plots on south-facing slopes had higher dissimilarity than those on north-facing slopes (Figure 4c; $p < 0.001$). We confirmed the importance of these predictors with a PERMANOVA (Appendix S9). The direction of the environmental vectors in the NMDS ordination also support the importance of these predictors for pre- and post-disturbance understory community (Appendix S10).

3.2 | Response of tree seedlings

The average density of *A. lasiocarpa* seedlings after the disturbance was significantly lower ($p = 0.002$; 5 ± 3 seedlings) than prior to the disturbance (7 seedlings per 0.01 ha vs 12 seedlings per 0.01 ha; Figure 5a). The change in *A. lasiocarpa* seedling density between sampling periods was positively related to the change in understory cover (Figure 5b; $p = 0.012$), such that the decline in seedling density became smaller as the change in understory cover increased. The change in *A. lasiocarpa* seedling density was not significantly predicted by the change in canopy cover, although a weak negative trend was detected (Figure 5c; $p = 0.051$).

Abies lasiocarpa seedling density was positively related to understory cover (Appendix S11a; $p = 0.025$) and negatively related to canopy cover (Appendix S11b; $p < 0.001$) before the disturbance but not after (Appendix S11a,b; Appendix S12). The median seedling densities for *A. lasiocarpa* were similar both before and after disturbance (Figure 5a; 8 vs 7 seedlings per ha respectively). However, the variance associated with seedling density decreased after the disturbance.

The average density of *P. engelmannii* seedlings did not change significantly ($p = 0.705$) in response to disturbance (Figure 5d; 1 seedling per 0.01 ha both before and after disturbance). The change in *P. engelmannii* seedling density was not predicted by either the change in understory cover or the change in canopy cover (Figure 5e,f). In addition, *P. engelmannii* seedling density was not related to understory cover or canopy cover before or after the disturbance (Appendix S11c,d). The direction and significance of our results for our seedling density models for both *Picea* and *Abies* did not change when examining all seedlings from 10 to 137 cm (Appendix S13).

3.3 | Species-specific responses

Species-specific responses to disturbance were significantly related to pre-disturbance frequency (priority effects), plant height at maturity, and leaf turgor loss point (Figure 6; Appendix S14). Models containing only pre-disturbance frequency or only species' traits did not have AIC values within two delta AIC of our final model containing a combination of both (Appendix S14). Three species (*Vaccinium scoparium*, *Erigeron peregrinus*, and *Ribes montigenum*) were collectively responsible for 67% of understory cover following disturbance (Figure 6a). The positions of these three species are labeled in Figure 6c–f. Shrubs were the most abundant growth form before

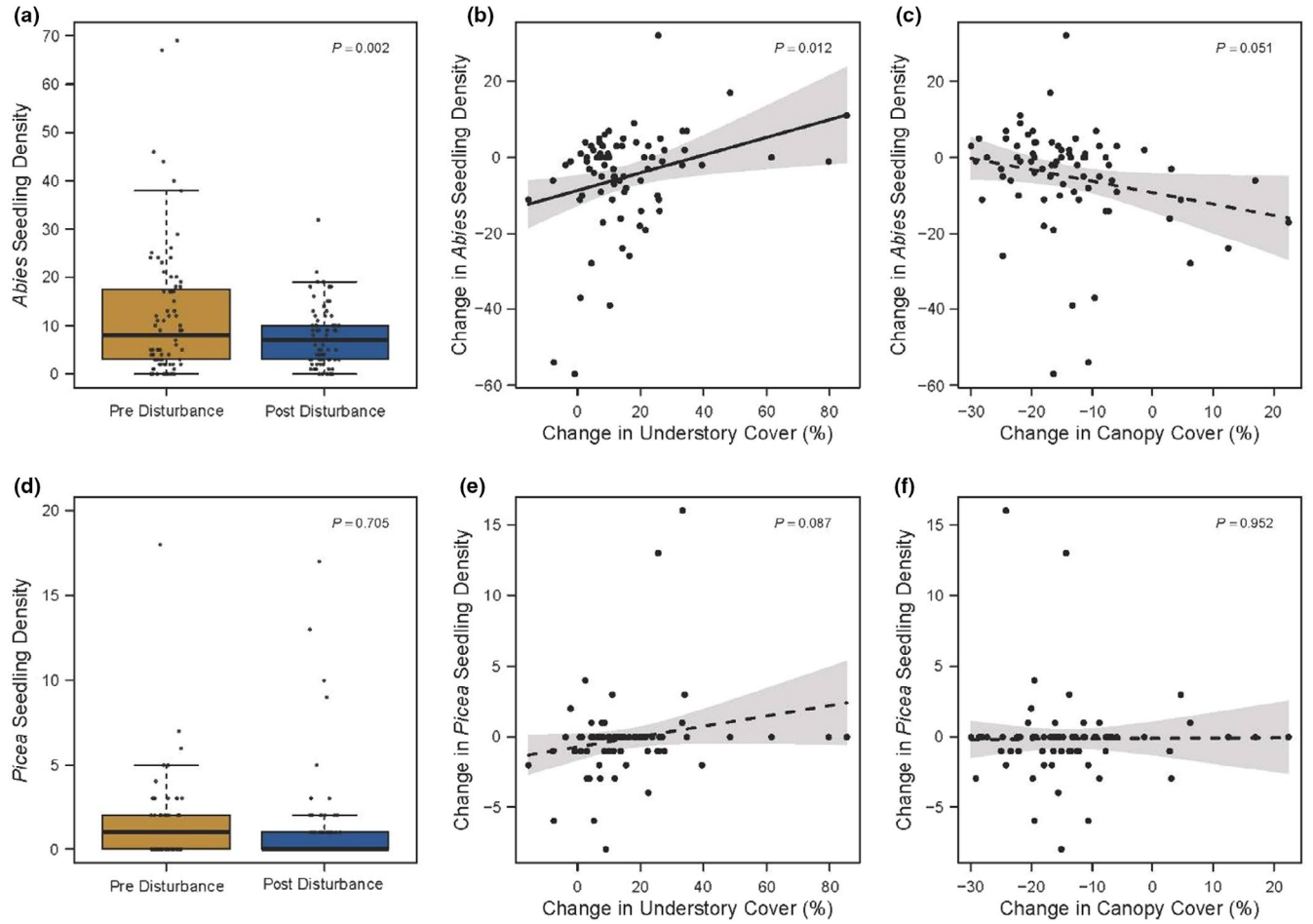

FIGURE 5 *Abies lasiocarpa* (a–c) and *Picea engelmannii* (d–f) seedling densities before and after a spruce beetle outbreak (a, d), and in response to disturbance as a function of the partial effects of change in understory cover (b, e) and change in canopy cover (c, f). Shaded areas represent 95% confidence intervals. Dashed lines represent non-significant trends. The model to predict change in *Abies* seedling density had an $R^2 = 0.15$, whereas the model used to predict the change in *Picea* seedling density had an $R^2 = 0.04$ (Summary of model results are in Appendix S12, observed vs predicted plot of model statements are found in Appendix S15j,m)

and after the disturbance (Figure 6b). Of the 46 common understory species examined for species-specific responses, two shrubs, *Vaccinium scoparium* and *Ribes montigenum*, were responsible for 73% of total pre-disturbance vegetative cover and 62% of total post-disturbance vegetative cover (Figure 6a). However, all growth forms (forbs, graminoids, and shrubs) exhibited net increases in cover following disturbance (Figure 6b). In our study, forbs also experienced a doubling in cover, graminoids experienced an approximate fivefold increase in cover, and shrubs increased in cover by only approximately 35%. The change in cover for individual species was positively related to their frequency prior to disturbance ($p = 0.002$); species that were more frequent prior to disturbance increased in cover the most after disturbance (Figure 6c). Change in species cover was positively related to plant height at maturity ($p = 0.011$); taller species increased in cover the most following disturbance (Figure 6d). Leaf turgor loss point was negatively related to change in species cover ($p = 0.035$); species with a more negative turgor loss point increased the most in cover following disturbance (Figure 6e). Change in cover was not significantly related to specific leaf area, although a weak positive trend was found (Figure 6f; $p = 0.061$). Leaf dry matter content and dispersal mechanisms were unrelated to the change in species cover (data not shown). Observed vs predicted plots for every model are presented in Appendix S15.

4 | DISCUSSION

The response of the understory plant community to widespread *Picea* mortality has been understudied despite evidence that the understory is important for carbon cycling (Misson et al., 2007), forest regeneration (Pettit et al., 2019), and wildlife habitat (Davis et al., 2020; Przepióra et al., 2020). To understand how the understory plant community responded to widespread *Picea* mortality in southeastern Wyoming, we quantified changes in understory cover and richness, tree seedling densities, and understory species responses to disturbance. The understory plant community increased significantly in cover and richness following canopy mortality by spruce beetles (Figures 1, 2a and 3a), which has several implications. First,

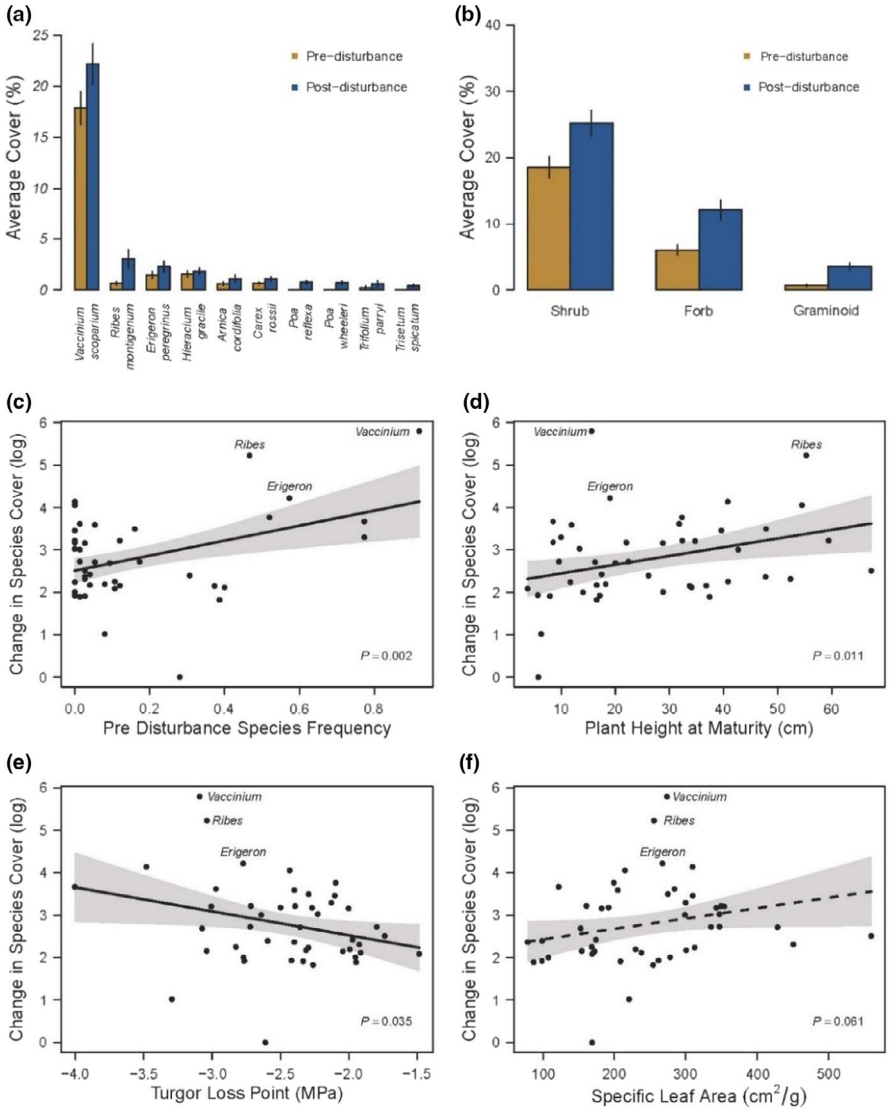

FIGURE 6 Cover for the 10 most frequent species before and after disturbance (a), and cover by growth form before and after the disturbance (b). Partial effects of species' response to disturbance are shown as a function of pre-disturbance species frequency across all plots (c), plant height at maturity in cm (d), leaf turgor loss point in MPa (e) and specific leaf area as cm^2/g (f). Shaded areas represent 95% confidence intervals and dashed lines represent non-significant trends. This model, which included the partial effects of these four predictors, explained 39% of the variation in responses (Summary of model results are in Appendix S14, observed vs predicted plot of model statements are found in Appendix S15n). The three most abundant species are labeled (c–f)

increases in understory cover and richness reflect the ability of the understory plant community to respond to spruce beetle disturbance. Second, the increase in understory cover, and respective increase in leaf area, support the hypothesis that increases in understory leaf area can contribute to carbon cycling in these forests. Third, increases in understory cover are associated with smaller declines in seedling densities for *A. lasiocarpa* following the disturbance, suggesting understory cover may influence forest regeneration. Fourth, increases in understory richness may be important to local pollinators (Davis et al., 2020) and other wildlife communities following disturbance by increasing the diversity of plant resources available to them. Finally, priority effects, as measured by species' pre-disturbance frequency, as well as the traits plant height at maturity and leaf turgor loss point were predictors of species' responses to disturbance suggesting that a variety of factors are responsible for variation in species responses.

Disturbance severity, as represented by the reduction in basal area, was expected to be a strong predictor of the change in understory community cover and species richness following spruce beetle mortality as observed after fires (Laughlin & Fulé, 2008; Romme et al., 2016), western balsam bark beetle outbreaks (McMillin et al., 2003), and mountain pine beetle outbreaks (Edwards et al., 2015; Pec et al., 2015; Pappas et al., 2020; Runyon et al., 2020). The increase in understory community cover that we observed is most similar to the effects of western balsam bark beetles on the understory community in a comparable forest in northeastern Wyoming (McMillin et al., 2003). In *P. engelmannii–A. lasiocarpa*-dominated stands affected by a western balsam bark beetle outbreak, a pairwise comparison of affected and unaffected plots showed that understory forbs doubled in abundance, whereas understory shrubs and graminoids increased approximately fivefold (McMillin et al., 2003). Comparing results of this study with those of McMillin et al. (2003), the similar magnitude of response for both forbs and graminoids (Figure 6b) regardless of disturbance agent is particularly noteworthy, especially when considering that plant community response to disturbance is highly variable (White & Jentsch, 2001). This suggests that understory plant communities can respond similarly to canopy mortality. The difference in the response of understory shrubs between our study and McMillin et al. (2003) may be attributed to high pre-disturbance shrub abundance across all sampled plots at GLEES;

compared with low pre-disturbance abundance of the same species, likely with comparable trait values, measured by McMillin et al. (2003), which may have limited the ability of shrubs to experience a fivefold increase in our system.

In this study, disturbance severity was not a significant predictor of the change in understory species richness following disturbance. However, elevation and aspect, which likely influenced *Picea* mortality (Coulson, 1979), were significant predictors of species richness. Lower elevations and south-facing aspects are generally warmer and drier than higher elevations and north-facing slopes (Peet, 1978) and provide favorable habitat for spruce beetles (Vega & Hofstetter, 2015), which likely influenced the spatial extent of spruce beetle infestation and the reduction in basal area (Coulson, 1979; Bentz et al., 2010; Dhar & Hawkins, 2011). In addition, the warmer and drier conditions may serve to extend the short growing season in the subalpine and allow for additional opportunities for new plants to establish.

Understory plant communities are important for ecosystem carbon cycling following mountain pine beetle outbreaks (Misson et al., 2007; Reed et al., 2014), and fire (Lavoie et al., 2010). In early phases of the disturbance, the forest at GLEES had relatively constant rates of carbon flux despite overstory mortality (Speckman et al., 2015). The consistency in the carbon flux may be explained in part by increased understory cover and subsequent carbon sequestration in vegetation. Increases in understory cover are especially important for subalpine *P. engelmannii*–*A. lasiocarpa* forests that are not likely to return to pre-disturbance conditions for decades to centuries (Veblen et al., 1991).

Understory cover was seen to increase within 10 years, whereas overstory species will be regenerating for decades following the spruce beetle disturbance (Derose & Long, 2010; Pettit et al., 2019). Pettit et al. (2019) observed that advanced regeneration of *Picea* was positively associated with understory cover 20 years following a spruce beetle outbreak. In addition, understory communities at the tree line were shown to have facilitative effects for tree seedling survival (Loranger et al., 2017). The microsite conditions (such as the reduction of climatic moisture deficits) that facilitate the establishment and growth of conifer seedlings are correlated with understory vegetation (Pettit et al., 2019). However, our results show that *Picea* seedling densities were not positively associated with the change in understory cover after the spruce beetle outbreak. Our results show that increases in understory cover are associated with lesser declines in seedling densities of *Abies* (Figure 5b,e). It is possible that this trend was observed for *Abies* seedlings and not *Picea* seedlings because *Abies* seedlings were more abundant than *Picea* seedlings before the disturbance (Figure 5a,d) so the influence of understory cover was more apparent. Importantly, increases in understory cover were not associated with decreases in seedling density for either species, and thus understory cover does not appear to competitively exclude seedlings.

The increase in understory species richness may increase pollinator diversity (Rhoades et al., 2018; Davis et al., 2020). Our results are consistent with those reported by Davis et al. (2020), suggesting that plant communities are more favorable for pollinators after spruce beetle outbreaks due to a reduction in basal area and increase in species richness. Pollinator diversity itself is important for the assembly and diversity of plant communities (Fontaine et al., 2006). Other invertebrate and vertebrate species may be responding to overstory mortality and increases in species richness and understory cover. Standing dead trees (snags), and increased ground cover may foster significant increases in avian species richness, diversity, and relative abundance by increasing the availability of suitable habitats (Przepióra et al., 2020).

Both priority effects and functional traits influenced the increase in understory plant cover with priority effects being the single greatest predictor (Appendix S14). The species that increased the most in cover after the disturbance were common in our plots prior to the disturbance. However, because species' pre-disturbance frequency was likely influenced by their functional traits, our metric of priority effects as a neutral model is not a perfect representation of a species response to disturbance driven by their inertia independent of identity. Priority effects are well documented as being important for overstory regeneration and community assembly in forested communities (Turner et al., 1998; Corbin & Holl, 2012; Buma et al., 2019; Solarik et al., 2020; Weidlich et al., 2021). Notably, priority effects have been used to understand the succession of overstory tree species (Turner et al., 1998; Solarik et al., 2020), and plant communities after a primary disturbance event (Buma et al., 2019). In both cases, priority effects were important for determining community composition. Priority effects have also been well documented for understory species, primarily in the context of restoration (Weidlich et al., 2021). In our study, priority effects were a significant predictor of a species' increase in cover following disturbance; however, it is possible that as overstory tree species regenerate understory composition will return to its pre-disturbance condition (Veblen et al., 1991; Derderian et al., 2016). Alternatively, because seedling densities of *A. lasiocarpa* were much greater than *P. engelmannii*, a shift to an overstory composition that is more *A. lasiocarpa* dominated may be likely and may alter understory plant community assembly. The duration of *A. lasiocarpa* dominance and long-term effects from this altered trajectory are unknown.

The three species that increased the most in cover after the disturbance were *V. scoparium*, *E. peregrinus*, and *R. montigenum*, all of which were abundant prior to the disturbance. Because these three species accounted for 83% of understory cover before the disturbance, dispersal would likely not be limited by the disturbance. Dispersal mechanism was not an important variable in explaining changes in abundance. Alternatively, because the understory at GLEES is dominated by perennial species, it may be expected that recruitment survival is low or unpredictable (Friedman, 2020). In addition, other dispersal related traits such as spreading through rhizomes or seed mass may be more important predictors (Westoby et al., 2002), but these were not available for this study. Taller species tended to exhibit larger increases in cover after the disturbance. As canopies opened in the years after the disturbance, species that could grow tall and acquire light that was previously limiting were

likely at a competitive advantage (Canham et al., 1990; Navas & Violle, 2009; Westerband & Horvitz, 2017).

The three species that increased the most had trait values associated with a low leaf turgor loss point inferring drought tolerance. Although the subalpine is not normally water limited because precipitation may occur in any month of the year (Regan et al., 1998), poorly developed soils with low water-holding capacity can result in dry conditions in late summer and early autumn. Plants with a more negative leaf turgor loss point would be able to tolerate these drier conditions and extend the length of their short growing season. In addition, increases in forest vapor pressure deficits could result in higher transpiration rates that favor plants with lower turgor loss points and lower water loss. Vapor pressure deficit was seen to increase following a mountain pine beetle outbreak in an even-aged lodgepole pine (*Pinus contorta*) forest in Wyoming (Reed et al., 2014). However, the structure of uneven-aged *P. engelmannii*–*A. lasiocarpa* forests may diminish the increase in vapor pressure deficit following disturbance. Alternatively, changes in the hydrologic budget of the forest may also be influencing species response to disturbance. Frank et al. (2019) saw an increase in total snowpack as a result of decreased canopy interception and sublimation within the subalpine forest at the GLEES. Although plant dehydration and freezing are different stressors, higher solute concentrations also prevent cell damage during freezing (Crowe et al., 1990), potentially conferring a fitness benefit in an ecosystem with cold and short growing seasons. More research is needed to understand how changes in the hydrologic cycle as a result of spruce beetle disturbance affect understory plant growth and survival.

In summary, we provide empirical evidence that understory plant community cover and richness increased a decade after canopy mortality caused by spruce beetles. The increase in understory plant cover likely contributes to the resiliency of carbon cycling in this system which will subsequently be of increased importance as epidemic beetle outbreaks are predicted to increase (Seidl et al., 2017). There is support for understory cover buffering a reduction in *A. lasiocarpa* seedling densities, but not for *P. engelmannii*. Importantly, there is no evidence to suggest the response of the understory plant community competitively excludes overstory seedlings. Finally, functional traits and priority effects were important predictors of species response to disturbance. Understanding the mechanisms responsible for driving species response to disturbance will allow for generalizable predictions of species' responses to other similar disturbances.

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AUTHOR CONTRIBUTIONS

PJF and DCL conceived the study. PJF and KAD collected the data in 2010–2012; TAC and PJF collected the data in 2019–2020. TAC and DCL developed the hypotheses and analyzed the data. TAC and DCL led the writing of the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the US Forest Service Research Data Archive (https://doi.org/10.2737/RDS-2022-0016).

ORCID

Trevor A. Carter https://orcid.org/0000-0002-8727-5327
Paula J. Fornwalt https://orcid.org/0000-0002-5252-408X
Daniel C. Laughlin https://orcid.org/0000-0002-9651-5732

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Latin names, functional groups, and functional traits of plant species.

Appendix S2. List of covariates included in global models.

Appendix S3. Results of separate PERMANOVAs comparing 1989 understory conditions to 2010.

Appendix S4. Summary of understory cover model results.

Appendix S5. Trajectories of understory cover before and after disturbance.

Appendix S6. Summary of species richness model results.

Appendix S7. Trajectories of species richness before and after disturbance
Appendix S8. Summary of Bray–Curtis dissimilarity model results
Appendix S9. Results of a PERMANOVA analysis for plant community composition
Appendix S10. NDMS ordination of plant community composition.
Appendix S11. Trajectories of *Abies* and *Picea* seedling densities before and after the disturbance.
Appendix S12. Summary of seedling density model results.
Appendix S13. Summary of seedling density model results that include all sizes 10–137 cm.
Appendix S14. Summary of mechanism of response model results.
Appendix S15. Observed vs predicted plots for all models used in our analysis

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