Plant Soil
https://doi.org/10.1007/s11104-025-07463-x

RESEARCH ARTICLE

Fine-root traits coordinate with aboveground strategies yet poorly predict species' response to spruce mortality

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Received: 28 February 2025 / Accepted: 9 April 2025

Abstract

Aims Fine-root traits are important for understanding the strategies plant species use to coexist in communities and persist in resource-limited environments. The extent to which aboveground and belowground strategies are coordinated is a continued subject of debate, and the role of fine-root traits in determining species responses to disturbance is largely unknown.

Methods We measured fine-root traits representing the conservation and collaboration axes of the root economics space and leaf traits associated with the leaf economics spectrum of 56 understory species across 75 plots that experienced a canopy opening disturbance 10 years prior in Wyoming, USA. We used principal component analysis to assess the coordination of aboveground and belowground strategies, and linear models to assess the relative importance of aboveground and belowground traits at explaining the change in understory species cover.

Responsible Editor: Benjamin M. Delory.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-025-07463-x.

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Published online: 14 April 2025

Results Traits related to the leaf economics spectrum (leaf dry matter content, leaf nitrogen) and the root conservation axis (root nitrogen, root tissue density) aligned with each other, but were orthogonal to the root collaboration axis (root diameter, specific root length) and aboveground plant height. Fine-root traits did not explain any additional variation in the response of understory species cover to disturbance beyond the variation explained by vegetative height and pre-disturbance species frequency.
Conclusions We provide further evidence for the coordination of aboveground and belowground economics strategies. Our results suggest that competition for light is more important than competition for resources belowground following the widespread disturbance that opened the canopy but did not physically perturb the soil or understory.

Keywords Belowground functional traits · Fine-root traits · Forest disturbance · Spruce beetle · Root economics space · Conservation gradient · Collaboration gradient

Introduction

Functional traits can predict the presence of plant species in local communities as they represent strategies that have successfully passed through the filters of community assembly (Laughlin and Laughlin 2013; Poddar et al. 2024). Differences in average trait values among species demonstrate the diverse plant strategies for persistence (Ding et al. 2024; Li et al. 2024; Wang et al. 2023). For example, leaf traits on the conservation gradient (Wright et al. 2004), improved our understanding of plant responses to ecosystem disturbance (Carter et al. 2022; Prado Júnior et al. 2015). However, our understanding of the importance of belowground traits as drivers of species' responses to ecosystem disturbance is just beginning (Freschet et al. 2021; Laughlin et al. 2021; Vleminckx et al. 2021). This is due in part because root traits in many local floras have not been quantified, leaving a wide avenue of inquiry underexplored.

Fine-root traits vary along two orthogonal axes in a root economics space that explains the belowground resource acquisition strategies of roots: the collaboration and conservation gradients (Bergmann et al. 2020; Matthus et al. 2025). The collaboration gradient ranges from species with high specific root length (SRL) that employ a "do-it-yourself" strategy of nutrient acquisition to species with large fine-root diameters (RD) that "outsource" nutrient acquisition to mycorrhizal fungi (Bergmann et al. 2020). Fine-roots also vary along a conservation gradient that ranges from more conservative to more acquisitive resource use (Bergmann et al. 2020). Species may have traits that facilitate rapid growth at the expense of root longevity, such as high root nitrogen concentration (RN); alternatively, species may have high root tissue density (RTD), which is associated with slower growth and conservative resource use (Berntson 1994; Caplan et al. 2017).

The coordination of above- and belowground plant strategies is a subject of current debate (Bueno et al. 2023; Weigelt et al. 2023). There is evidence that aboveground and belowground functional traits related to resource acquisition (specifically nitrogen) are coordinated along a whole plant economics spectrum (Ding et al. 2024; Reich 2014; Weigelt et al. 2021, 2023), whereas other work has concluded that aboveground and belowground economics strategies are independent (Carmona et al. 2021). A lack of consensus is due in part to the need to compare functionally analogous above- and belowground traits (Weigelt et al. 2023). Further insight into the relative coordination of plant strategies can be obtained by systematically quantifying species-level functional traits of more species in more environments. Specifically, species that experience changes in aboveground and belowground resource availabilities, such as those subjected to ecosystem disturbance, can provide valuable insight into plant resource strategies (Kumordzi et al. 2019).

Research on trait-disturbance relationships has largely focused on aboveground traits, such as leaf-height-seed traits (e.g., Strahan et al. 2015), which can provide insight into how understory species utilize resources. For example, increases in light availability following forest disturbance may correspond with increased cover for taller understory plant species that are more competitive for light (Carter et al. 2022). However, this is a relatively one-dimensional view: disturbances also impact belowground resources such as water availability (Frank et al. 2019) and nutrient availability (Boggs Lynch et al. 2021; Speckman et al. 2015). Fine-root trait strategies are increasingly recognized as important for understanding plant

strategies for persistence along climatic (Laughlin et al. 2021; Wang et al. 2023), hydrologic (Li et al. 2024; Taseski et al. 2021), and competitive (Dabu et al. 2024) gradients, but much less is known about how they shape plant recovery following disturbance. Disturbance events, such as fires, insect outbreaks, or logging, can determine the structure and composition of vegetative communities by altering the spatial and temporal availability of both aboveground and belowground resources (Jentsch and White 2019; Pettit et al. 2019; Su et al. 2019). Belowground traits may be important in structuring the understory plant community after disturbance (Taseski et al. 2021), especially if belowground structures remain intact following disturbances. The relatively discrete nature of disturbance events leads to pulses of aboveground and belowground resources that can promote variability in the ecological strategies used to acquire resources (Kumordzi et al. 2019). Bark beetle disturbances such as spruce beetle outbreaks are occurring at unprecedented scales (Barrett and Robertson 2021; Biedermann et al. 2019; Seidl et al. 2017) and provide an excellent opportunity to understand the role of root traits in predicting plant community responses to broad scale ecosystem disturbance.

Spruce beetle outbreaks kill overstory trees while leaving an intact understory that is impacted by changing conditions, particularly increased light (Carter et al. 2022; Davis et al. 2020). For example, 10 years after widespread spruce mortality in a subalpine forest, understory plant community cover increased, and community composition was altered both through the addition of new species and changing abundances of species already present (Carter et al. 2022). Species that were most abundant prior to the outbreak benefited the most, and species with taller heights at maturity and higher osmotic resistance to wilting increased in cover (Carter et al. 2022). Spruce beetle outbreaks also impact belowground conditions, changing soil nutrients, pH, moisture, temperature, and microbiome (Custer et al. 2020; Mikkelson et al. 2013; Norton et al. 2015), likely affecting understory plant composition and structure. Available soil nitrogen can increase due to needle drop in the years following a spruce beetle outbreak (Boggs Lynch et al. 2021; Speckman et al. 2015). Additionally, the removal of canopy cover likely increases soil temperature and moisture in the years following disturbance (Boggs and Mcnulty 2010; Gray et al. 2002; Su et al. 2019), which can correspond with increases in species with higher SRL capable of rapid exploitation of soil resources (Wang et al. 2023). Increases in both nitrogen availability and the forest floor temperature have been shown to stimulate understory fine-root production and decrease fine-root mortality in a forest with a cold and short growing season (Majdi and Ohrvik 2004). We still do not understand the relative importance of root traits in explaining understory species responses to disturbances such as spruce beetle outbreaks in forests.

Here, we quantified fine-root traits for 56 species in the understory plant community in a recently disturbed subalpine spruce-fir forest in the Southern Rocky Mountains. Specifically, we asked the following questions: 1) Do we see evidence for a two-dimensional root economics space (i.e., a collaboration and conservation gradient) in the understory flora and are root and leaf economics spectra coordinated? 2) Do fine-root traits (RTD, RN, SRL, and RD) predict more variation in species level changes in cover from spruce beetle disturbance than aboveground traits and pre-disturbance species frequency (Carter et al. 2022)? We predicted that fine-root traits aligned with the collaboration and conservation gradients would be orthogonal (Bergmann et al. 2020) but that leaf and root conservation traits would be aligned in this subalpine flora (Ding et al. 2024; Weigelt et al. 2021). Given the loss of the dominant canopy species (*Picea engelmannii*), soil nutrients and water are likely broadly available. Further, because soil nutrient availability likely increased through needle drop (Boggs Lynch et al. 2021) and moisture availability likely increased through decreases in canopy sublimation (Frank et al. 2019), we predicted that species with more acquisitive fine-root traits such as high RN and SRL would increase in abundance after the spruce beetle outbreak as these species are more capable of rapidly acquiring inputs in belowground resources.

Materials and methods

Study site description

We conducted our study within and adjacent to a 600-ha experimental site (Glacier Lakes Ecosystem Experimental Site) in the Medicine Bow National

Forest, southern Wyoming, U.S.A. (Fig. S1). Across the sampled elevation gradient (3200–3500 m), forest soils are generally rocky and shallow and dominated by quartzite (Musselman et al. 1994). All sampling occurred within the dominant dry subalpine forest plant community (Regan et al. 1998). In the mid to late 2000 s and early 2010 s, a widespread epidemic spruce beetle outbreak occurred throughout subalpine forests in western North America, including this study site, which experienced losses upwards of 80 m^2/ha in spruce basal area (Carter et al. 2022; Frank et al. 2014; Hart et al. 2014; Morris et al. 2015).

Data collection

We measured understory plant species cover and richness within 75 permanent, randomly distributed plots in both 2010 and 2020 that span a gradient from 0 to 100% overstory mortality (Carter et al. 2022). The 2010 sampling event occurred immediately after the onset of the spruce beetle outbreak, yet this sampling reflects pre-outbreak understory plant conditions as the community was not significantly different from the community documented during the 1980 s (Carter et al. 2022). The 2020 sampling event reflects understory plant conditions a decade after the outbreak. We measured plant cover for all understory species in 15 Daubenmire quadrats (20 ×50 cm), with five evenly spaced along three 5.64 m transects per plot. We report cover to the nearest percentage, which we averaged within transects and then across them.

We collected above and belowground species-level functional trait data for 56 understory plant species (Table 1; Table S1). The 56 species (41 forbs, 12 graminoids, and 3 shrubs) occurred in at least 2 of the 75 plots and cumulatively represent 95% of post outbreak species cover and 85% of species occurrences in 2020, above the 80% suggested minimum species coverage from Pakeman and Quested (2007). We used previously published aboveground trait data for specific leaf area (cm^2/g; SLA), leaf dry matter content (g/g; LDMC), vegetative height at maturity (cm), and leaf turgor loss point (MPa; TLP) for 46 species collected in the study area during 2020 (Carter et al. 2022). We collected aboveground trait data for an additional 12 species in 2021 consistent with the methods used previously (Carter et al. 2022). We measured species' height in the field before we collected leaf samples. We rehydrated leaf samples

Table 1 Table of the traits measured, their common abbreviations, units, and a brief description on their ecological importances, primarily as they relate to resource acquisition

Trait	Abbreviation	Description
Vegetative Height	Height (cm)	The maximum vegetative height measured at maturity. Species with taller vegetative heights are often exposed to higher amounts of incoming light
Leaf Dry Matter Content	LDMC (g/g)	A trait along the conservation gradient of the leaf economics spectrum. Species with high LDMC invest heavily in leaf architecture. These leaves are longer lived and exhibit a more conservative resource acquisition strategy
Specific Leaf Area	SLA (cm^2/g)	A trait along the conservation gradient of the leaf economics spectrum. Species with high SLA have low leaf longevity but high capacity for resource acquisition
Leaf Turgor Loss Point	TLP (MPa)	The point at which leaves are no longer able to maintain cell pressure when dehydrated. Species with more negative TLP are more drought tolerant
Leaf Nitrogen Concentration	LN (%)	The concentration of nitrogen found within the leaf. More leaf nitrogen is associated with more acquisitive leaves
Root Diameter	RD (mm)	A trait along the collaboration gradient of the root economics space. Species with higher RD are those that outsource resource acquisition to associated mycorrhizae
Specific Root Length	SRL (m/g)	A trait along the collaboration gradient of the root economics space. Species with higher SRL exhibit a do-it-yourself strategy of belowground resource acquisition
Root Tissue Density	RTD (g/cm^3)	A trait along the conservation gradient of the root economics space. Species with higher RTD invest in fine-root architecture, increasing fine-root longevity at the cost of rapid resource acquisition of belowground resources
Root Nitrogen Concentration	RN (%)	A trait along the conservation gradient of the root economics space. More root nitrogen is associated with more acquisitive fine-roots

to full turgor for measurements of SLA, LDMC, and TLP. We estimated TLP using the vapor pressure osmometer method (Bartlett et al. 2012) which records osmolarity within a leaf. Osmolarity was then converted into leaf turgor loss point through linear relationships developed for forbs, graminoids, and woody species (Griffin-Nolan et al. 2019). In addition to the traits measured in Carter et al. (2022), we measured leaf nitrogen concentration (%; LN) for all 56 species (n = 3 replicates/species) by oven drying leaf tissue samples at 60 °C for 48 h before being analyzed for elemental analysis using a Costech elemental analyzer.

We collected 3 fine-root tissue samples from distinct individuals for all 56 species in the field by excavating whole root systems when possible. We stored the samples in damp paper towels for transportation before being stored at 5 °C prior to analysis. We cleaned and weighed fine-root samples, defined as non-suberized first, second, and third order roots according to McCormack et al. (2015). We used these fine-root samples to measure root diameter (mm; RD), root length, and root volume using a WinRhizo scanner (Epson Smart-Scan). We dried fine-root samples at 60 °C for 48 h before weighing samples to calculate root tissue density (g/cm^3; RTD), root dry matter concentration (g/g; RDMC), and specific root length (m/g; SRL). We also used these oven-dried fine-root samples to determine root nitrogen concentration (%; RN) using a Costech elemental analyzer.

Statistical analysis

All statistical analyses were performed in R version 4.4.1 (R Core Team 2024) using functional trait data that was first checked for degree of intraspecific variation to ensure interspecific variation was greater than intraspecific variation (Fig. S2), which was then averaged to the species level. To understand the dimensionality of functional trait space for this understory subalpine flora, we used a principal component analysis (PCA) that included fine-root traits that align with resource conservation (RN and RTD) and collaboration (SRL and RD; Bergmann et al. 2020), as well as traits that capture major variation in aboveground strategies such as the leaf economics spectrum (LN and LDMC; Blumenthal et al. 2020; Wright et al. 2004), and light acquisition (vegetative height at maturity; Weigelt et al. 2021; Westoby 1998). Within the PCA, we categorized species by functional group and presence in sampling period (present in 2010 or absent in 2010) to provide insight into different strategies within our flora. We then compared the bivariate relationships of traits associated with each of the major axes of variation using Pearson's correlation coefficients to assess the strength of expected conservation and collaboration trade-offs.

To test the hypothesis that root traits predicted understory species response to spruce beetle caused forest disturbance, we fit four linear models with a Gaussian error structure using cube root transformed change in cover (percent cover in 2020—percent cover in 2010) as the response. We used cube root transformations because we had (1) negative changes in cover (species declined in cover), (2) biologically meaningful zero values which would not be appropriately captured using a log transformation, and (3) biological outliers that would be overrepresented in the data with a square root transformation. We first constructed an intercept only model (null model) that we use to conduct pairwise evaluation for our other three models using log-likelihoods based on model information criterion in the AICcmodavg package (Mazerolle 2023). Our other three models included: 1) the response of understory plant cover predicted by belowground traits (SRL, RD, RTD, RN), 2) the response of understory plant cover predicted by aboveground traits (LDMC, SLA, TLP, height, LN), and pre-disturbance species frequency (priority effects) based on Carter et al. (2022), or 3) a global model that predicted the response of understory plant cover using aboveground traits (LDMC, SLA, TLP, height, LN), belowground traits (SRL, RD, RTD, RN) and pre-disturbance species frequency.

Results

Dimensionality of subalpine flora trait space

Functional traits in this forest understory subalpine flora could be reduced to three independent dimensions in the principal component analysis (Fig. 1), because the first three eigenvalues derived from the correlation matrix were > 1 (Table 2). These three dimensions accounted for 72% of the variation in the trait data (Table 2). The first principal component represented a whole plant economics

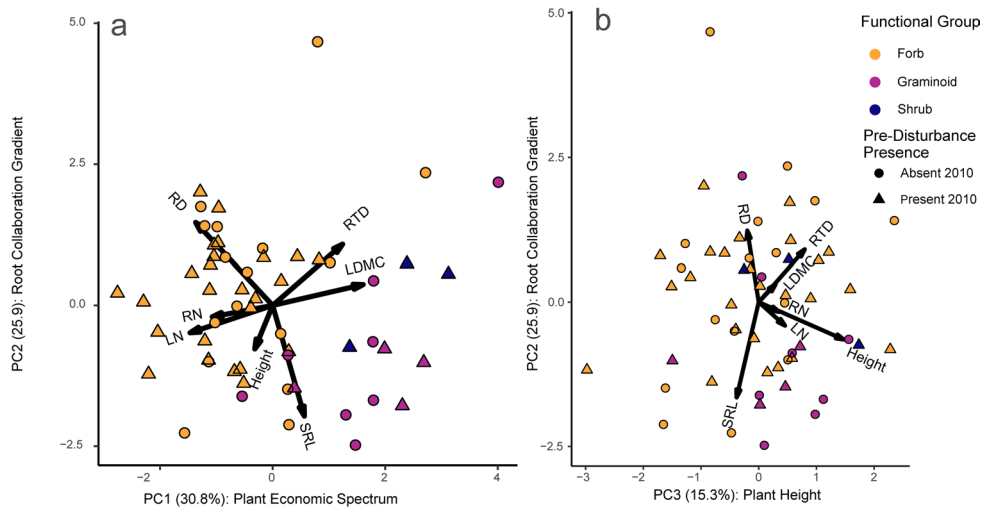

Fig. 1 Principal component analysis where shapes indicate whether species were observed in the post-disturbance sampling period, and shape color indicates functional groups. See Table 2 for associated eigenvalues and eigenvectors. Arrows represent the loadings of each trait onto the PCA: LDMC = leaf dry matter content; Leaf N = leaf nitrogen concentration; Height = vegetative height at maturity; RTD = root tissue density; Root N = root nitrogen concentration; SRL = specific root length; RD = root diameter

Table 2 Summary of results from the principal component analysis (PCA). We report the eigenvalues, proportion of variance explained, and eigenvectors for principal components one (PC1), two (PC2), and three (PC3)

		PC1	PC2	PC3
	Eigenvalues	2.16	1.82	1.07
	Proportion of Variance	31	26	15
	Cumulative Proportion	31	57	72
Plant trait axes:	Eigenvectors:			
Leaf economics	Leaf Dry Matter Content	0.516	− 0.129	0.159
	Leaf N Concentration	− 0.471	0.170	0.247
Root conservation	Root Tissue Density	0.399	− 0.377	0.432
	Root N Concentration	− 0.344	0.071	0.192
Root collaboration	Specific Root Length	− 0.181	0.687	− 0.207
	Root Diameter	− 0.439	− 0.512	− 0.107
Whole plant	Plant Height	− 0.102	0.270	0.798

spectrum, where species on the high end of the axis exhibited high LDMC and RTD and low RN and LN. The second principal component represented the root collaboration gradient generated by a tradeoff between SRL and RD. Vegetative height at maturity loaded separately onto the third principal component. Bivariate correlations indicated a weak negative relationship between LN and LDMC and a strong negative relationship between RD and SRL. However, there was no significant relationship between RN and RTD (Fig. S3), despite exhibiting a trade-off in multidimensional trait space (Fig. 1).

We did not observe any distinct grouping of functional groups in trait space (Fig. 1), nor did any of the functional groups respond more to the spruce beetle outbreak (Fig. S4). Further, we did not observe a difference in the strategies for species found in both sampling periods compared to the species that were only detected in the post-outbreak sampling period,

as evidenced through no distinct groupings of shapes across any of the principal components (Fig. 1).

Do fine-roots explain understory plant change in cover?

RTD, RN, SRL, and RD were poor predictors of understory species' responses to spruce beetle outbreak (Figs. 2, 3, and Table 3). Fine-root traits from the root collaboration and conservation gradients had weak predictive power. This was evident in both the belowground traits model (Fig. 2; Table S2) and the global model, which included aboveground traits, pre-disturbance species frequency, and belowground traits (Table S2). In both cases, fine-root traits did not influence changes in understory plant cover, with effect sizes near zero and large standard errors (Fig. 2). The model that used belowground functional traits to predict changes in understory species cover only explained 5.9% of the variance in the response variable (Table S2).

In contrast, the aboveground functional trait model explained 34.6% of the variance and the global model explained 38.2% of the variance in the data (Table S2). The change in species cover was positively correlated with vegetative height at maturity and pre-disturbance species frequency (Figs. 2, 3, and Table S2). Despite explaining the most variance in the data, the global model was not the most likely model of the four models that

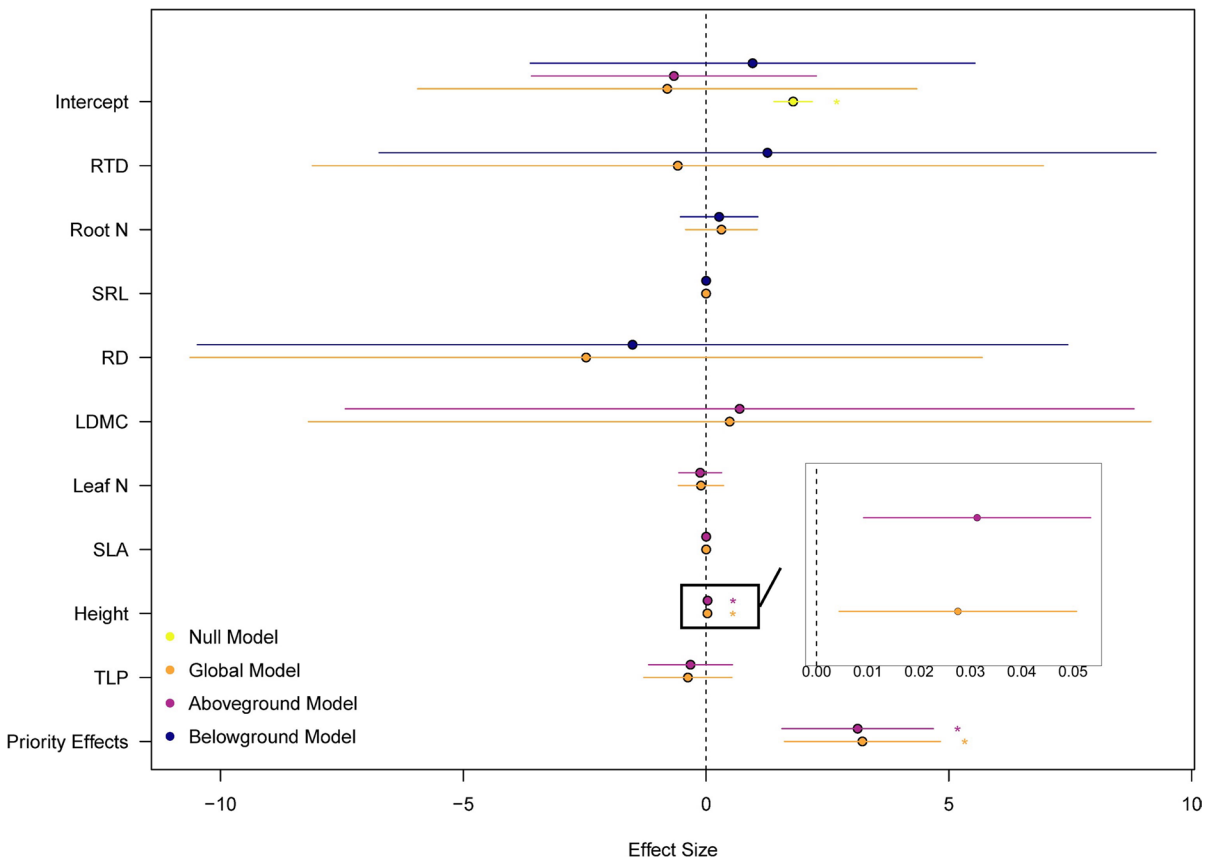

Fig. 2 Effect sizes (model coefficients with 95% confidence intervals) from each of the four models constructed to test the importance of potential mechanisms. See Table 3 for associated AIC and evidence ratios. Points represent average effect sizes and segments correspond with 95% confidence intervals. Statistically significant effects ($P < 0.05$) are denoted with an asterisk (*). See Table S2 for a full summary of model results. Possible explanatory variables include the following: Priority effects = species pre-disturbance frequency; TLP = leaf turgor loss point; height = vegetative height; SLA = specific leaf area; Leaf N = leaf nitrogen concentration; LDMC = leaf dry matter content; RD = root diameter; SRL = specific root length; Root N = root nitrogen concentration; RTD = root tissue density

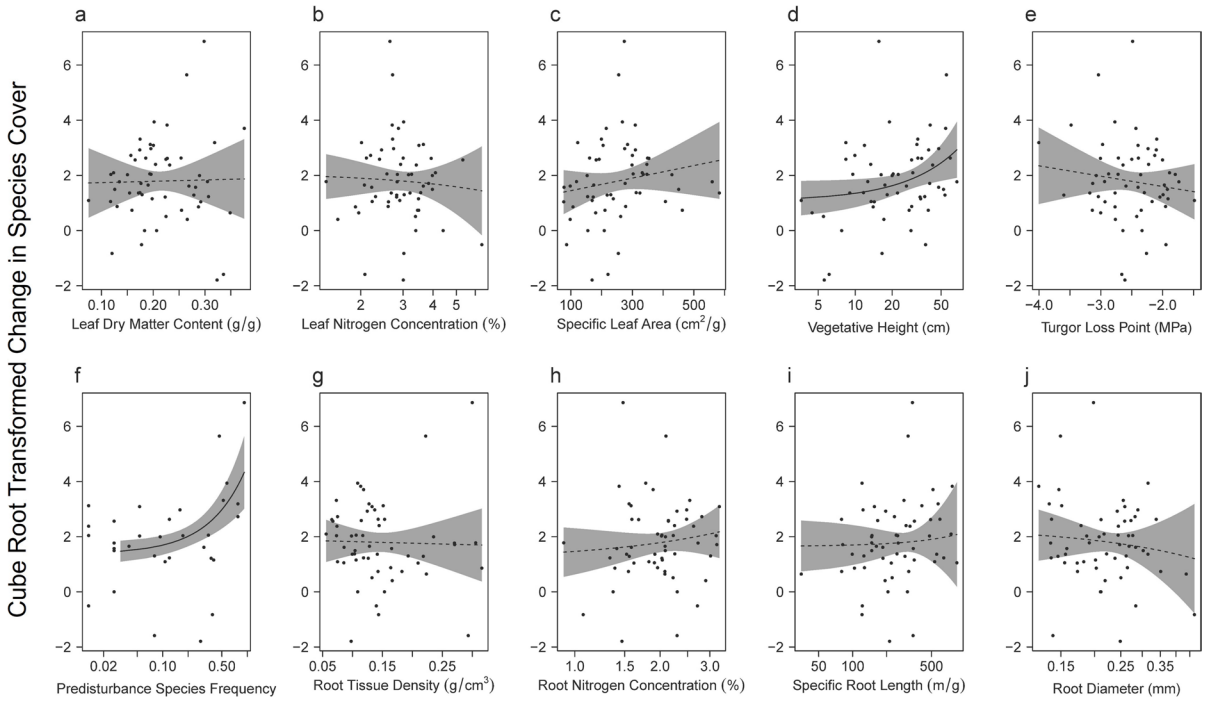

Fig. 3 Partial effects from the global model that uses leaf dry matter content (**a**), leaf nitrogen concentration (log scale) (**b**), specific leaf area (**c**), vegetative height at maturity (log scale) (**d**), leaf turgor loss point (**e**), pre-disturbance species frequency (log scale) (**f**), root tissue density (**g**), root nitrogen concentration (log scale) (**h**), specific root length (log scale) (**i**), and root diameter (log scale) (**j**) to predict the cube root transformed change in species cover. Aboveground traits (except leaf nitrogen concentration) and pre-disturbance species frequency represent previously tested potential mechanisms from Carter et al. (2022)

Table 3 A summary of AICc model averaging for the null model, aboveground traits and pre-disturbance species frequency model, belowground trait model, and global model (Table S2). *K* number of estimated parameters, *AICc* information criterion, *Delta AICc* change in information criterion, *AICc Weight* model probabilities indicating the level of support in favor of any given model among the candidate models. Cum. Weight cumulative information criterion weights, LL log likelihood of each model. Evidence ratios represent the pairwise comparison of evidence of each model as compared to the belowground trait model. Values greater than 1 represent increased likelihood of occurring while values less than one represent decreased likelihood of occurring

AICc model average comparisons							
Model	K	AICc	Δ AICc	AICc weight	Cum. weight	LL	Evid. ratio
Null Model	2	208	8.98	0.010	0.990	− 102	1.00
Global Model	12	208	9.04	0.010	1.00	− 88.3	0.970
Aboveground Traits	8	199	0	0.980	0.980	− 89.8	89.1
Belowground Traits	6	214	15.1	0.000	1.00	− 100.1	0.050

we fit to have generated the data. In comparison to our null model, the model that included only aboveground traits was the most likely model to have generated the data (Table 3) and was 89 times more likely to have generated the data than the null model. The null model was the next most likely to have generated the data, with both the global model and belowground trait model being less likely than the null model to have generated the data (Table 3).

Discussion

Understanding the role of root traits in driving the response of the understory plant community to spruce beetle outbreaks is important because it enhances our ability to make generalizable predictions of species responses to other widespread disturbances. Spruce beetle outbreaks promote changes in microclimate that are distinct from other disturbance types, allowing us to evaluate the role that functional traits play in disturbance response while providing testable hypotheses linked to first principles and enhancing our mechanistic understanding of forest understory recovery. Species-specific long-term data collected before and after disturbance is rare and provides a unique opportunity to examine the mechanisms that determine species responses to disturbance. By measuring the traits of species that have not been included in previous analyses, we demonstrate the existence of the two-dimensional root economics space in a new species assemblage —this understory subalpine flora— and show that leaf economics traits were coordinated with the root conservation axis. Surprisingly, none of our hypotheses on the role of root traits in driving species responses to spruce beetle outbreak were supported. Fine-root traits provided poor predictive power for the response of the understory. These results imply that aboveground competition for light may be more important than belowground competition for nutrients following the removal of the spruce canopy by spruce beetles.

Dimensionality of trait space

There is considerable debate about whether aboveground and belowground plant traits are independent or coordinated (Bueno et al. 2023; Carmona et al. 2021; Weigelt et al. 2021, 2023). Our results agree mostly with Weigelt et al. (2021), who argued for coordination of economics traits (especially nitrogen concentration) from roots to leaves but recognized the existence of other independent strategy dimensions (e.g., vegetative height).

First, leaf economics traits were coordinated with fine-root conservation traits. Traits associated with resource economics both above- and belowground (LDMC, LN, RTD, RN) all loaded on the first principal component. This observation conforms with a whole plant economic spectrum (Ding et al. 2024; Reich 2014; Weigelt et al. 2021, 2023). In other words, species that have more conservative fine-root traits (higher RTD and lower RN) also had more conservative leaf traits (higher LDMC and lower SLA), suggesting coordination of above- and belowground strategies. The whole plant economics spectrum was only detected within the context of a multidimensional analysis because the bivariate correlation between RTD and RN was not significant. Interestingly, although interspecific variation was greater than intraspecific variation for all functional traits measured, both RTD and RN displayed the highest level of intraspecific trait variation (Fig. S2), which may account for the lack of a bivariate correlation. RN and RTD have been observed to have high intraspecific variation at fine spatial scales in an arctic flora (Fraterrigo et al. 2024) and intraspecific variation in these traits may be driven by shifts in soil water concentration and available nitrogen (Li et al. 2024). Spruce beetle outbreaks can modify both nitrogen (Boggs Lynch et al. 2021) and water resources (Frank et al. 2019; Manning et al. 2021), although the effect of these modifications on intraspecific variation of RTD and RN in this system remains unknown.

Second, consistent with both Weigelt et al. (2021) and Carmona et al. (2021), we found evidence for a two-dimensional root economics space (Bergmann et al. 2020; Kramer-Walter et al. 2016). Traits from the root collaboration gradient (SRL and RD), loaded onto a second principal component that was independent from traits on the root conservation gradient (RTD and RN). Therefore, this subalpine flora conforms to the general pattern of a two-dimensional fine-root economics space, adding to the rapidly growing body of evidence for this commonly observed pattern (Matthus et al. 2025).

Third, plant height was independent from all other leaf and root traits measured in this study. This finding is consistent with previous studies that outline an independent axis of plant growth form (Weigelt et al. 2021; Westoby 1998). The observation that height was the only trait that was correlated with the response of the understory to spruce beetle outbreak indicates that the competition for light is likely more important than resource uptake following canopy-opening disturbances. This is likely due to the sparse nature of understory communities in closed-canopy systems which are primarily light limited.

Explanatory power of fine-root traits following spruce beetle outbreak

SRL, RD, RTD, and RN represent traits along the two major axes of fine-root trait variation (Bergmann et al. 2020), but none were important predictors of the understory plant community response to spruce beetle outbreak in this subalpine forest. Aboveground plant height and pre-disturbance species frequency were the strongest explanatory factors for the response of the understory plant community to the spruce beetle outbreak (Carter et al. 2022). These results suggest that competition for light aboveground is more important than competition for resources belowground following the widespread spruce beetle induced tree mortality. Plant height is an indicator of how well a species competes for light, and light was likely the resource that changed the most following a disturbance that opened the canopy but induced no immediate physical perturbation to the soil or understory. Changes to soil water and nutrient availability likely did occur shortly after this spruce beetle outbreak (Boggs Lynch et al. 2021; Frank et al. 2019; Manning et al. 2021). However, belowground resources were likely not limited prior to the outbreak, thus increases in their availability had a limited effect on community composition. We would expect fine-root traits to explain more changes in community composition if soil water and nutrient changes had a stronger effect on plant responses to the disturbance. Alternatively, the traits that we measured along the conservation and collaboration gradients may not represent the most important strategies understory plant species use to respond to disturbance in this system. Understory species subjected to experimental warming and nitrogen addition in a similar cold spruce forest in Norway showed decreased risk of root mortality and increases in fine-root production (Majdi and Ohrvik 2004). Neither of which we directly measured in this study but warrant study in future investigations.

Importantly, our global model and aboveground traits and pre-disturbance species frequency model only explained 38.2% and 34.6% of the variation respectively, leaving a substantial amount of variation (over 60%) unexplained. There may be a mismatch between the timescale when we measured functional traits and species cover after spruce beetle induced tree mortality, and the timescale that would be able to capture variability in fine-root traits. The similarity between functional traits for species found before the disturbance and species found after the disturbance was unexpected given the known alterations to belowground resources that occur following spruce beetle outbreaks (Boggs Lynch et al. 2021). Understory plant community traits are more plastic in the months to few years following pulses of resources into the soil environment (Kramer-Walter and Laughlin 2017) and the effect of resource alterations grow weaker in the decades following spruce beetle outbreaks, despite their legacies being present on the landscape (Boggs Lynch et al. 2021). Thus, it is possible that our observed fine-root trait values would slightly but meaningfully differ during shorter time scales. It will be important to carefully consider how disturbance events alter environmental filters to plant community assembly and not only select appropriate functional traits to measure but also match the temporal scales of research to the temporal scale that plant communities are responding to the disturbance.

It is unlikely that belowground traits play no role in the structuring of understory plant communities in subalpine spruce-fir forests. These systems are marked by short growing seasons and the plant communities are composed of many perennial species (Regan et al. 1998), which typically leads to high root:shoot ratios that are indicative of higher investment in belowground biomass (Rydin et al. 1999). However, changes in belowground biomass of understory species after bark beetle disturbance are largely undocumented. Understory species may allocate more biomass to belowground structures than easily observable aboveground biomass in the years to decades following spruce beetle induced tree mortality. This would also help to explain why pre-disturbance species frequency and aboveground functional traits, specifically vegetative height, are important predictors as we collected data on aboveground plant cover (as opposed to belowground biomass or root:shoot ratio) to use as the response variable.

Conclusions

In summary, we provide evidence of coordination between aboveground and belowground plant economic strategies, as well as independent axes including fine root collaboration and whole plant height, in this subalpine flora. Empirical evidence suggests that fine-root traits along the collaboration and conservation axes

of the root economics space are not good predictors of the response of understory species cover to widespread spruce mortality a decade after peak overstory mortality. This may be due to (1) a greater importance of competition for light, (2) a possible mismatch between the impacts of the spruce beetle outbreak on belowground resources and the observed change in aboveground plant cover, or (3) inappropriate selection of belowground traits. Future research on plant functional traits and disturbance will need to investigate both the near and long timescales to elucidate the effect of changing belowground resources on the strategies that plant species use to respond to disturbance.

Acknowledgements We thank the University of Colorado Denver department of Integrative Biology and the University of Wyoming Botany department for their support. We thank Dr. John Frank and John Korfmacher for their logistical assistance during the 2010 and 2020 field seasons, and we thank Stephanie Asherin, Marin Chambers, Ellen Michelson, Roger Tyler, Mason Parcus and Carl LaNore for their assistance with data collection.

Author contributions TAC, PJF, and DCL conceived the study. PJF and KAD collected 2010 understory community data. PJF and TAC collected 2020 understory community data. TAC collected the 2020 functional trait data. TAC, AES, KRH, and SAW collected 2021 functional trait data. TAC constructed models with help from JRF and DHA. All authors contributed significantly to manuscript drafts and review.

Funding This work was supported by the USDA Forest Service, University of Colorado Denver, and University of Wyoming.

Data availability The datasets generated during and/or analyzed during the current study are available in the supplement of this manuscript (Table S1).

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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