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Root and biomass allocation traits predict changes in plant species and communities over four decades of global change

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Abstract

Global change is affecting the distribution and population dynamics of plant species across the planet, leading to trends such as shifts in distribution toward the poles and to higher elevations. Yet, we poorly understand why individual species respond differently to warming and other environmental changes, or how the trait composition of communities responds. Here we ask two questions regarding plant species and community changes over 42 years of global change in a temperate montane forest in Québec, Canada: (1) How did the trait composition, alpha diversity, and beta diversity of understory vascular plant communities change between 1970 and 2010, a period over which the region experienced 1.5°C of warming and changes in nitrogen deposition? (2) Can traits predict shifts in species elevation and abundance over this time period? For 46 understory vascular species, we locally measured six aboveground traits, and for 36 of those (not including shrubs), we also measured five belowground traits. Collectively, they capture leading dimensions of phenotypic variation that are associated with climatic and resource niches. At the community level, the trait composition of high-elevation plots shifted, primarily for two root traits: specific root length decreased and rooting depth increased. The mean trait values of high-elevation plots shifted over time toward values initially associated with low-elevation plots. These changes led to trait homogenization across elevations. The community-level shifts in traits mirrored the taxonomic shifts reported elsewhere for this site. At the species level, two of the three traits predicting changes in species elevation and abundance were belowground traits (low mycorrhizal fraction and shallow rooting). These findings highlight the importance of root traits, which, along with leaf mass fraction, were associated with shifts in distribution and abundance over four decades. Community-level trait changes were largely similar across the elevational and temporal gradients. In contrast, traits typically associated with lower elevations at the community level did not predict differences among species in their shift in abundance or distribution, indicating a decoupling between species- and community-level responses. Overall, changes

were consistent with some influence of both climate warming and increased nitrogen availability.

INTRODUCTION

Studies have shown widespread responses of organisms to global environmental change, including shifts in abundance (Vellend et al., 2017), distribution (Chen et al., 2011; Kelly & Goulden, 2008; Lenoir et al., 2008), and taxonomic diversity (Harrison et al., 2015; Parmesan & Yohe, 2003; Pauli et al., 2012). Some of the important gaps remaining in our understanding of plant response to global change can be filled by studying plant traits.

First, syntheses have reported temporal changes in local taxonomic diversity, with increases and decreases equally likely (Dornelas et al., 2013; Vellend et al., 2013), but it is unclear whether these results apply to changes in trait composition and diversity as well. Yet, trait composition and diversity are argued by many to be more directly relevant than taxonomic composition and diversity to ecosystem function and dynamics, especially in plants (Diaz et al., 2007; Garnier et al., 2016; Lavorel & Garnier, 2002). Second, species respond somewhat idiosyncratically to environmental change (e.g., warming or nutrient deposition), with species varying in the magnitude (Chen et al., 2011; Feeley et al., 2011; Talluto et al., 2017) and even direction of their response (Bobbink, 2004; Crimmins et al., 2011; Hallbäcken & Zhang, 1998). Beyond some general tendencies in species' responses, such as upward elevational and latitudinal shifts in distribution in response to warming (Becker-Scarpitta et al., 2019; Dullinger et al., 2012; Lenoir et al., 2008; Rumpf et al., 2018), we have a limited ability to predict which species will "win" or "lose" the global change challenge. Indeed, identifying which traits affect performance (growth, survival, and reproduction) along environmental gradients has been identified as one of the current frontiers in trait-based plant ecology (Laughlin & Messier, 2015; Salguero-Gómez et al., 2018; Shipley et al., 2016). Last, studies of species' responses to environmental change over time remain quite rare relative to studies of responses over spatial gradients (Dornelas et al., 2013; Vellend et al., 2013), and our ability to use spatial patterns to make temporal predictions is uncertain (Fukami & Wardle, 2005; Johnson & Miyanishi, 2008; Pickett, 1989).

To address some of these knowledge gaps, we combine the measurements of above- and belowground traits with a dataset of forest understory vegetation change over 42 years (Savage & Velend, 2014). At the community level, we ask how plant trait composition, alpha diversity, and beta diversity of plots located along an elevational gradient have changed during this period (Table 1, Question 1). At the species level, we ask how well, and which, traits predict changes in species abundance and distribution (Table 1, Question 2). During the period of our study (1970–2012), the study site in southern Québec, Canada, has been characterized by marked warming, which appears to be an important cause of vegetation change (Becker-Scarpitta et al., 2019). Last, we take advantage of the fact that our dataset covers both spatial and temporal climatic gradients of similar magnitude to ask whether spatial and temporal trait–environment relationships are similar (Table 1, Question 3).

To answer these questions, we measured whole-plant, leaf, and root traits for the 36–46 most abundant understory species in the temperate forest of Mont-Mégantic National Park, Québec, Canada, where species relative abundances were previously surveyed in forty-eight 400–800 m^2 plots (for coniferous and deciduous stands, respectively) in 1970 and 2012 (Savage & Velend, 2014). We selected traits capturing leading dimensions of trait variation as well as physiological function expected to affect species' niches. Over this 42-year period, local mean annual temperature increased by ca. 1.5°C and precipitation regimes did not change (Appendix S1: Section S1). Total wet nitrogen deposition is estimated to have decreased over that period (Environment and Climate Change Canada, 2023; Likens et al., 2021). However, given that fertilization from atmospheric nitrogen deposition has been documented to affect vegetation worldwide (Bobbink et al., 2010), and that wet deposition rates at the site over the study period (8–15 kg of total nitrogen ha^{-1} year^{-1}) are around the critical deposition thresholds for temperate forests (10–20 kg of total nitrogen ha^{-1} year^{-1}), plants were likely affected by nitrogen deposition during this period. Global models and a local time series for the region and for nearby sites (Hubbard Brook, New Hampshire) show this region experienced a marked increase in atmospheric nitrogen deposition rates from ~1.5 kg ha^{-1} year^{-1} since the industrial revolution, followed by a plateau between the 1970s and the 1990s, and then a subsequent decline (Hember, 2018; Lamarque et al., 2013;

T A B L E 1 Set of questions and predictions tested, along with associated results and related materials.

Predictions	Supported	Results	Related materials
Question 1. How has the trait composition of communities changed over time?			
Within communities			
Prediction 1a. Trait composition: CWMs of high-elevation plots shifted toward low-elevation values	Yes	lme: ↑veg. height, ↑rooting depth, ↓lamina thickness, ↑LDMC, ↑leaf area, ↑LMF, ↓SRL, ↑mycorrhizal fraction; PERMANOVA: $p < 0.001$, $R^2 = 0.25$	Figures 1 and 2; Appendix S1: Table S6
Prediction 1b. Trait diversity within plots (alpha diversity) increased	Yes and no	F_{RICH} ↑: 1970 = 10.5; 2012 = 26.2; paired t-test: $p < 0.001$; F_{DISP} similar: 1970 = 1.8; F_{DISP} 2012 = 1.9; paired t-test: $p = 0.29$	Figure 1B
Among communities			
Prediction 1c. Trait similarity among plots along elevation ↑ (beta diversity ↓)	Yes	F_{DISP} ↓: 1970 = 0.115; 2012 = 0.051; PERMDISP: $p = <0.001$	Figure 2
Prediction 1d. CWM–elevation relationships weakened	Yes	One-tailed paired t-test: $t = -1.5$, $p = 0.08$	Figure 1A; Appendix S1: Table S6
Question 2. Do traits predict species abundance and elevational changes over time? If so, which traits?			
Prediction 2a. Traits predict species response over time			
Abundance response	Yes	glm: Deviance explained = 0.54, $p = 0.09$; regression tree: Deviance explained = 0.29	Figure 3A; Appendix S1: Table S8
Elevation response	Yes	lm: Adjusted $R^2 = 0.34$, $p = 0.02$; regression tree: Deviance explained = 0.47	Figure 3B; Appendix S1: Table S9
Prediction 2b. Traits associated with warm environments at the community level also predict species response over time (community-species coherence)			
Abundance response	No	glm: Increase in abundance associated with low mycorrhizal fraction (pseudo R^2 = ca. 33%)	Figure 3A; Appendix S1: Table S8
Elevation response	Yes and no	lm: Increase in elevation associated with shallow rooting depth and high LMF (adjusted R^2 = ca. 40%)	Figure 3B; Appendix S1: Table S9
Question 3. Do communities respond similarly to spatial and temporal gradients?			
Prediction 3. Spatial and temporal CWM–elevation relationships are similar (spatio-temporal coherence)	Yes	lme: Effects of time and elevation on trait values are opposite and significant for all traits	Box 1; Appendix S1: Table S7

Abbreviations: CWM, community-weighted mean; F_{DISP}, functional dispersion; F_{RICH}, functional richness; glm, generalized linear model; lm, linear model; lme, linear mixed-effects model.

Likens et al., 2021). Because nutrients can accumulate in the soil over time and because the study species live for many decades, it is unclear how these changes have affected the amount of nitrogen available for plants at the time of the two surveys. Thus, although we do not have the same temporal and spatial resolution for nitrogen availability as we do for temperature (Appendix S1: Section S1), we consider the possibility that vegetation changed in response to changes in nitrogen availability. It is likely that the elevational gradient changed over time because high elevations experience both greater nutrient limitation (higher C:N ratio and thinner organic layer; Carteron et al., 2020) and greater nitrogen deposition rates (Weathers et al., 2006). In the broader region, a potentially important driver of temporal vegetation change is land use (Danneyrolles et al., 2019). However, it is unlikely that land use drives vegetation changes at our study site because Mont-Mégantic was established as a protected area shortly after the first vegetation survey, the study plots were established in

largely undisturbed forest, and its land use history is well documented. Hence, this factor is not considered further.

Earlier studies at this site were focused exclusively on taxonomic composition and diversity. Savage and Velend (2014) found an average uphill shift of 36 m in species distributions, which lagged behind the 300-m uphill shift in temperature isoclines. Species showed a large variability in the magnitude and direction of their elevational shifts. The total number of understory species across plots increased by 12% (86 species in 1970; 96 in 2012), and the average species richness within plots increased by 25%. Species composition homogenized along the elevational gradient, driven by the composition of high-elevation communities shifting toward that of low-elevation communities.

We tested predictions about trait changes at the community and species levels. At the community level (Table 1, Question 1), assuming that some traits reflect species' adaptations to climatic and resource niches (Caruso et al., 2020; Geber & Griffen, 2003; Gutschick & BassiriRad, 2003), we expect trait responses to mirror the taxonomic responses reported by Savage and Velend (2014). Specifically, we predict that: (Prediction 1a) community trait composition has shifted, with community-weighted mean (CWM) traits shifting toward low-elevation trait values (i.e., values more frequent at low elevation); (Prediction 1b) the trait diversity within communities increased; (Prediction 1c) trait composition of plots homogenized along the elevational gradient, with trait values of high-elevation communities shifting over time toward low-elevation values. As a corollary, we also predicted that (Prediction 1d) the slope of the CWM–elevation relationship should weaken over time. Predictions 1c and 1d hold if community shifts are lagging behind climate shifts, as suggested by the findings of Savage and Velend (2014).

At the species level (Table 1, Question 2), if species traits reflect adaptation to their climatic and resource niches, and if species changes in elevation and abundance over time are partly driven by change in climate and resources, we expect that traits will predict species elevational and abundance response over time (Table 1, Prediction 2a). Because changes in community trait composition result from changes in species presence and relative abundance, those traits that changed at the community level should also predict species response to warming (Prediction 2b). However, community-level analyses using CWM are abundance-weighted and therefore, all else being equal, strongly influenced by the most abundant species (Clark, 2016), but species-level analyses equally weigh all species, most of which have low abundance. Thus, this prediction only holds if the same traits determine the climatic and resource niches of species of low and high abundance. Last, if long-term temporal environmental changes mirror spatial gradients (Table 1, Question 3), then community-level trait changes over time should mirror changes along the elevational gradient (Prediction 3).

Expectations for how individual traits and trait diversity might respond to warming and nitrogen deposition were drawn from the literature. Here we only report patterns from the same system, from global studies, or those emerging from our literature review as being consistent across systems. See Appendix S1: Section S2 for a description of the literature considered and for information on study systems and traits with mixed or sparse findings. For temperate understory plants, we expect maximum vegetative height to increase with soil fertility (and therefore with nitrogen deposition) (Amatangelo et al., 2014; Blondeel et al., 2020; Diekmann & Falkengren-Grerup, 2002; Maes et al., 2020; Perring et al., 2018), and with higher temperature (Amatangelo et al., 2014; Blondeel et al., 2020; Govaert et al., 2021; Maes et al., 2020; Vanneste et al., 2019). Leaf dry matter content (LDMC) is expected to decrease with soil fertility (Amatangelo et al., 2014). We expected leaf size to increase with both temperature (Moles et al., 2014) and precipitation (Fonseca et al., 2000; Givnish, 1987; Moles et al., 2014). In terms of root traits, specific root length is expected to increase with nutrient availability (Comas et al., 2002; Freschet et al., 2013; Holdaway et al., 2011; McCormack et al., 2012; Roumet et al., 2006) and to decrease with temperature (Freschet et al., 2017). Maximum rooting depth is expected to increase with warming and increased precipitation (Schenk & Jackson, 2002). The extent of mycorrhizal associations should decrease with soil fertility (Treseder & Vitousek, 2001; Wurzburger & Wright, 2015; but see Maes et al., 2020).

For alpha diversity, we expect positive effects of warming, because it relaxes the strong selection for cold tolerance that otherwise considerably narrows the range of viable trait values (Fischer, 1960; Swenson et al., 2012; Wieczynskiak et al., 2019). For nitrogen deposition, the effects on trait diversity are too variable across studies to make clear predictions (cf. Brown & Zinnert, 2021; Kermavnar et al., 2021). For beta diversity, we expected homogenization across the elevational gradient from species turnover given upslope distribution shifts of low-elevation species (Savage & Velend, 2014), and from changes in species relative abundance due to both warming and atmospheric deposition (see Appendix S1: Section S2).

METHODS

Study site

The study was conducted in Parc National du Mont-Mégantic, a 55-km^2 protected area located in southern Québec (45.4552° N, 71.1499° W). With a

ca. 650-m elevational gradient (ca. 450 to ca. 1100 m above sea level), vegetation shifts from northern hardwood forest dominated by sugar maple at low elevation to spruce–fir boreal forest on the summits (Hall, 1998). On one of the peaks, soil pH was reported to decrease with elevation from temperate to boreal forest type, C:N ratio and labile P increased, and the depth of the organic layer increased (Carteron et al., 2020). Within the park, localized natural disturbances occur periodically, including spruce budworm outbreaks (1974–1984) and ice storm damage (1998), but the park did not experience major anthropogenic changes between the two survey periods (Société des Établissements de Plein air du Québec [SEPAQ], 2007).

Using data from Natural Resources Canada (McKenney et al., 2006), we calculated that between 1970 and 2012 local mean annual temperature increased by ca. 1.5°C, precipitation regimes did not change, with the mean remaining around 1300 mm annually, the min and max growing season temperatures increased by 0.7 and 0.9°C, and growing season length increased by 12 days (Appendix S1: Figures S1 and S2). The combination of longer, warmer summers with constant summer precipitation has likely led to a decrease in net water availability to plants during their growth period. See Appendix S1: Section S1 for more information on change in climate between the two surveys.

Wet nitrogen deposition is estimated to have decreased from 12 to 15.5 kg ha^{-1} year^{-1} in 1981 to 8.0–10.5 kg ha^{-1} year^{-1} in 2017, with NH_4^+ remaining constant and NO_3^- decreasing (Environment and Climate Change Canada, 2023). See supplemental information for more details. This is consistent with national and international emission control measures implemented since 1980 have been reported to be successful in Europe and North America (Granier et al., 2011; Xing et al., 2013). These values do not include dry deposition such that total wet and dry depositions are likely to exceed the critical values for nitrogen deposition for temperate forests understories, estimated at 10–20 kg of total nitrogen ha^{-1} year^{-1} (Bobbink et al., 2010). Given that pre-industrial levels of total nitrogen deposition are estimated to be ~1.50 kg ha^{-1} year^{-1} (Hember, 2018; Likens et al., 2021), at the time of the first survey in 1970, the communities were likely already affected by nutrient enrichment.

Plant community data

In 1970, Marcotte and Grandtner (1974) recorded the presence and relative abundance of all plant species in 94 plots with areas of 400 m^2 (coniferous forests) or 800 m^2 (deciduous forest) in and around the area occupied by the current park. Relative abundances were estimated using Braun-Blanquet cover classes. In 2012, Savage and Vellend (2014) re-surveyed the 48 plots located within current park boundaries. These 48 plots, sampled at both time points, were used in all analyses. There was a total of 86 understory species across all plots in 1970 and 1996 in 2012 (Savage & Vellend, 2014). Seventeen species that were absent from the plots in 1970 were gained in 2012, typically at low occurrence (most in 1–3 plots; Appendix S1: Table S1), and seven species that were present in 1970 at low occurrence were lost in 2012 (in only 1–3 plots; Appendix S1: Table S2). According to more comprehensive park surveys (Hall, 1998) and current observations, these changes do not generally represent actual losses and gains from the regional pool, but likely result from stochastic changes in the distributions of low-abundance species. The Sorensen similarity index was 0.87 across years. Importantly, here we measured traits for the 46 most abundant species across both censuses such that none of our analyses were affected by any changes to the species pool.

Trait data

From May to August 2016, we characterized traits on 7–12 individuals of the 46 most abundant understory plant species (Appendix S1: Table S3). Together, these species form the majority of the understory communities (median percent cover in 1970 = 99.9%; min = 64.0%; max = 100%). All species are perrenials. Most species are forbs, but also include ferns, shrubs and clubmosses (Appendix S1: Table S3). We sampled individuals from populations located in Mont-Mégantic and nearby sites. On each individual, we measured a set of 11 traits characterizing different aspects of plant function and calculated species-level values (maximum for vegetative height and averages for all other traits). See Appendix S1: Section S5 for further method details.

The traits were chosen to capture some of the leading strategy dimensions organizing plant phenotypic diversity (Westoby et al., 2002) and other important attributes of plants (Poorter et al., 2012; Weemstra et al., 2016). To capture the leaf economic spectrum (Reich et al., 1999; Wright et al., 2004), we measured leaf mass per area (LMA; fresh weight per area, in grams per square centimeter), LDMC (dry weight per fresh weight; in grams per gram), and leaf thickness (lamina thickness per millimeter). To capture the maximum height dimension (Westoby, 1998), we measured the maximum vegetative height (in centimeters). To capture the leaf and twig size architectural dimension, we measured leaf area (in square

centimeters) (Olson et al., 2009; Westoby et al., 2002; White, 1983).

Strategy dimensions organizing root traits remain a frontier in trait-based ecology (Freschet et al., 2021; Weemstra et al., 2023) such that we measured a set of root traits affecting water and nutrient acquisition strategies. Recent work has identified the degree of reliance on mycorrhizal symbionts for resource foraging as the main axis distinguishing species root traits (Bergmann et al., 2020; Ma et al., 2018). We measured three traits associated with this axis: mycorrhizal fraction (the percentage of root length colonized by arbuscular mycorrhizae), specific root length (SRL; in centimeters per milligram), and fine root diameter (in millimeters). We also measured minimum and maximum rooting depth, which is often associated with water availability (Fan et al., 2017; Schenk & Jackson, 2002), but not always (Schulze et al., 1996; Nippert & Holdo, 2015). We used the following depth categories: 0 = humus top; 1 = mid-humus; 2 = humus bottom; 3 = hummus/mineral soil interface; 4 = ≤5 cm in mineral; 5 = >5 cm in mineral. To avoid the confounding issues that can arise when roots of different sizes and functions are compared, absorptive roots were defined as the fine roots of first and second order (Comas et al., 2002; McCormack et al., 2015; Pregitzer et al., 2002; Withington et al., 2006).

Last, we measured a biomass allocation trait, leaf mass fraction (LMF), which represents the fraction of aboveground plant biomass allocated to leaves (in grams per gram). Biomass allocation offers an alternative way to describe species ecology, where species allocate biomass to the organs capturing the most limiting resource (Freschet et al., 2015; Kramer-Walter & Laughlin, 2017; Tilman, 1988). LMF thus indicates the relative biomass allocated to capturing light, with the fraction of biomass allocated to leaves increasing with nutrient availability and decreasing with light (Poorter et al., 2012). To avoid collinearity in linear and generalized linear models (described in *Species-level changes*), we eliminated from all analyses three traits that were highly correlated with others: minimum root location, LMA, and fine root diameter (variance inflation factor >3), leaving a set of eight statistically independent traits. See Appendix S1: Section S5 for detailed methods of trait measurements, and Appendix S1: Figure S3 for a PCA showing the relationship among the studied traits.

Before calculating species' mean trait values, we tested whether the sampling date affected the trait values of individual plants for those traits with a significant date effect. We did so by running models predicting trait values from sampling date and species and assessing with an ANCOVA if the sampling date term was significant. It was found to be significant for LDMC and LMF, but the variance explained by sampling date was 0.3% and 0.1%, respectively, so we chose not to remove date effects. Because growth is a multiplicative process, traits reflecting size and growth (leaf area, vegetative height, and lamina thickness) were natural log-transformed (Kerkhoff & Enquist, 2009).

The 46-species dataset represents over 80% of the community in 47 of the 48 plots and over 90% in 45 plots (median percent cover in 1970 = 99.9%; min = 64%; max = 100%, Appendix S1: Section S1, Tables S4 and S5). Because we were not able to obtain root traits for the 10 shrub species and because principal component analyses cannot handle missing data, from the 46 species, a subset of 36 containing the root traits was used for all analyses. This subset of species still represents over 50% of the understory plant communities for 46 of the 48 plots, and 80% or more of the community for 29 of the 48 plots (median percent cover in 1970 = 88.5%; min = 42.9%; max = 100%; Appendix S1: Section S3, Tables S4 and S5). To confirm that this species subset did not qualitatively affect the results of the community analyses, we compared the results of all the community-level analyses (multivariate and regressions) obtained with the dataset containing all 46 species and five traits (no root traits), with the results obtained with the data subset containing 36 species and all 8 traits. We confirmed that both datasets produce qualitatively similar results. We present the results of the community-level analyses with the dataset of 36 species and all 8 traits because root traits were important in the species-level analyses, and this allows us to contrast species- and community-level patterns. To obtain meaningful community-weighted metrics, we recalculated relative abundance based on this species subset. Species-level trait values from those 36 measured species were used to calculate the CWMs of both 1970 and 2012.

Statistical analyses

Within-plot trait averages and diversity

To test the prediction that the trait composition of communities has shifted toward low-elevation traits (Table 1, Prediction 1a), we calculated the change in CWM for each trait in each plot along the elevation gradient in 1970 and 2012. We built linear mixed models predicting changes in community-weighted trait means as a function of elevation, year (binary variable), and their interaction, with plot as a random variable (lmer() function from lme4{} package) (Bates et al., 2015). Coding plot as a random variable effectively treats the two observations for a given plot as a pair. To examine community-level

trait changes from a multivariate perspective, we performed a permutational multivariate analysis of variance (PERMANOVA, adonis() function from vegan{} package, version 2.5-6) (Oksanen et al., 2019), with "year" as predictor. The PERMANOVA tests for a change in the multivariate trait composition (i.e., group centroids) of the plots between 1970 and 2012. We used the Bray–Curtis dissimilarity metric for multivariate analyses. We used nonmetric multidimensional scaling (NMDS) ordination to visualize multivariate changes over time in trait composition.

To test the prediction that trait diversity within communities has increased over time (Table 1, Prediction 1b), we first ran paired t-tests on plot-level metrics of trait diversity calculated for each survey (t.test() function from stats{} package). We calculated two multivariate trait diversity indices: functional richness (F_{RICH}), which does not take into account species abundances, and functional dispersion (F_{DISP}), which does (dbFD() function from FD {} package, version 1.0-12). Functional richness is measured as the convex hull volume in multivariate trait space, and functional dispersion computes the average distance to the trait centroid, weighted by species abundances (Laliberté et al., 2014). In contrast with CWMs, which solely reflect the central tendencies, functional diversity reflects variety and is affected by the range of trait values. CWMs, F_{RICH}, and F_{DISP} are thus complementary metrics.

Among-plot (beta) diversity

To test the prediction that the trait values of plots have homogenized over time (Table 1, Prediction 1c), we performed a permutational analysis of dispersion (PERMDISP, betadisper() function from vegan{} package, version 2.5-6). PERMDISP tests for change between 1970 and 2012 in across-plot trait homogeneity. To test the prediction that trait–elevation relationships became weaker (Table 1, Prediction 1d), for each trait we built a linear model predicting CWMs as a function of elevation, year (1970 or 2012), and their interaction (lm() function of the stats{} package), and assessed the significance of the year: elevation interaction term.

Species-level changes

For each species, we calculated change in abundance as the ratio of the average abundance across plots between the two surveys, because change in abundance (i.e., population growth) is a multiplicative process. For each survey, those average abundances across plots were calculated

as the average of the percent cover midpoints of Braun-Blanquet cover classes. The 46 species in this study did not include those that were only present in 2012 because they would have given an abundance ratio of infinity. Change in elevation between the two surveys was calculated as the difference in the mean elevation of each species for each survey, weighted by their abundance.

To test whether traits can predict change in species abundance and elevational distribution over time (Table 1, Prediction 2a), we first built regression trees (tree() function from tree{} package, version 1.0-40) (Ripley, 2019). To retain only the meaningful branches, we used the cv.tree() function from tree{} package (version 1.0-40) to optimally prune the tree. The function splits the data into a training set for model fitting and a validation set to evaluate goodness of fit. We ran 53 trials and selected the pruning depth that minimized the tree deviance most frequently.

In addition, we conducted a generalized linear model for change in abundance (glm() function from stats{} package, gamma family and log link) and a linear model for change in elevation (lm() function from stats{} package). The gamma distribution is appropriate for our abundance ratio, being lower bound at zero and positively skewed.

Before running these models, we followed the data exploration protocol outlined by Zuur et al. (2010) to avoid model misfit and statistical errors. As described in the Trait Data section, one of the three traits removed to avoid collinearity was LMA. Because LMA is one of the most commonly measured traits in plant ecology, we verified that excluding it did not change our results. To do so, we ran the same species-level analyses including LMA instead of lamina thickness and LDMC. The results were qualitatively similar. After model fitting, we verified model assumptions by plotting residuals versus fitted values, versus each covariate in the model and versus each covariate not in the model (Zuur et al., 2010). We also examined high-leverage data points to ensure that relationships were not due to a few species.

To test which traits predict species abundance and elevation shifts over time, in the linear and generalized linear models, we used an information theoretic approach, which is exploratory by nature. We first built a full model including the eight (noncollinear) traits. We then performed model selection on the eight traits as well as the trait–trait interactions detected in the regression trees in order to find the best models (dredge() function, MuMIn{} package version 1.43.15). We assessed model fit using corrected Akaike information criterion (AIC_c) (Barton, 2024). We avoided overfitting the best models by capping the number of parameters included in the model to four. This maintains a reasonable number of data

points per parameter (here, 36/4 = 9). All equivalent best models within two AIC_c units are reported. As this is an exploratory and not a hypothesis-testing approach, p values were not calculated; instead, we interpret consistent trends across the set of equivalent best models. All statistical analyses were performed in R (R Core Team, 2020).

RESULTS

How have community trait composition and diversity changed over time?

Within communities, both trait composition and diversity have significantly changed over time. In terms of trait composition, individual trait analyses showed that CWMs have increased in average vegetative height, rooting depth, leaf area, LMF, LDMC, and mycorrhizal fraction, and decreased in average SRL and lamina thickness (Appendix S1: Table S7). Figure 1A shows that the magnitude of changes increased with increasing plot elevation. The black arrows in Figure 1A highlight that the 2012 trait–elevation regressions flattened because the high-elevation plots shifted toward the trait values of low-elevation plots. For all traits, the slope of the relationship became shallower or nonsignificant over time (one-tailed paired t-test: $t = -1.5$, df = 7, $p = 0.08$; Figure 1A; Appendix S1: Table S6). Thus, the direction of temporal changes in trait values mirrored the spatial change in trait values from high to low elevation (Appendix S1: Table S7; Figure 1A), suggesting a temporal shift toward trait values associated with low elevations. Recent studies have found that the specific metrics (slope, intercept, p value, R^2) of CWM–environmental gradient relationships are sensitive to species turnover because species co-occurrence among plots can lead to reduced effective sample size and, in turn, to p value inflation (ter Braak, 2019; Zelený, 2018). Accordingly, we do not interpret individual statistics, but focus on the consistent overall qualitative changes in CWMs with elevation and time. Jointly examining the set of traits, the PERMANOVA indicated that CWMs shifted over time, mainly with respect to two traits: increased rooting depth and decreased SRL ($R^2 = 0.25$, F ratio = 31.6, $p = {<}0.001$; Table 1, Figure 2). Figure 2 also illustrates how these changes result from high-elevation plots shifting toward low-elevation trait composition.

In terms of changes in trait diversity, across the dataset, plot-level functional richness has more than doubled over time (F_{RICH} 1970 = 10.6 ± 0.60; F_{RICH} 2012 = 26.2 ± 2.5, paired t test $p < 0.001$), with the increase in functional richness occurring in low-elevation plots (Figure 1B). In contrast, functional dispersion, a diversity index accounting for species relative abundance, did not significantly increase (F_{DISP} 1970 = 1.8 ± 0.11, F_{DISP} 2012 = 1.9 ± 0.09, paired t test $p = 0.29$).

Among communities, the PERMDISP showed that plots have significantly homogenized, with the trait composition of communities at different elevations becoming more similar over time (Table 1, Figure 2). Specifically, trait dispersion among communities (beta diversity) has decreased by more than half, from 0.12 in 1970 to 0.05 in 2012 (F ratio = 41.0, $p < 0.001$). The trait composition of high-elevation plots shifted toward that of low-elevation and the latter remained similar over time. This multivariate homogenization along elevation is consistent with the relationship between elevation and the CWM of individual traits weakening over time.

Do traits predict species shifts in elevational and abundance?

The traits measured here were moderately successful at predicting species changes in abundance and elevational distribution over time. In terms of abundance, traits predicted roughly 30%–50% of the variation among species: the regression tree explained 29% of the deviance with optimal pruning at three splits (Table 1, Figure 3A), and the full glm explained 54% of the variance (although it was of marginal statistical significance, $p = 0.09$; Table 1 and Box 1, Panel A). In terms of elevation, traits predicted roughly 30%–50% of species variation in elevational shifts over time: the regression tree explained 47% of the deviance with an optimal pruning at two splits (Table 1, Figure 3), and the full linear model explained 34% of the variance ($p = 0.02$; Table 1, Figure 3A).

For each of elevation and abundance responses, the different analyses identified the same few traits as predictors of species shifts. First, the regression tree and generalized linear models both identified mycorrhizal fraction as the most important trait explaining species change in abundance (ca. 30%). Among the five models with an equivalently good fit to the data (within two AIC_c units), all included mycorrhizal fraction, including a model containing only this trait (Model No. 2). Species that increased the most in abundance had a low (<0.58) mycorrhizal fraction (Table 1, Box 1, Figure 3A). Second, the regression tree and linear models both identified LMF and rooting depth as the main traits explaining species elevational shifts (ca. 40%, Table 1, Figure 3B; Appendix S1: Table S8). Among the eight models with an equivalently good fit to the data (within two AIC_c), all included rooting depth and LMF. Species with higher LMF shifted more in elevation. The effect of rooting depth on
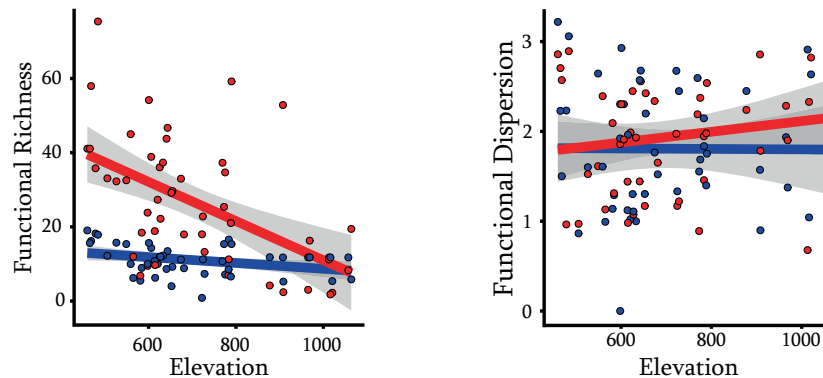
Panel A
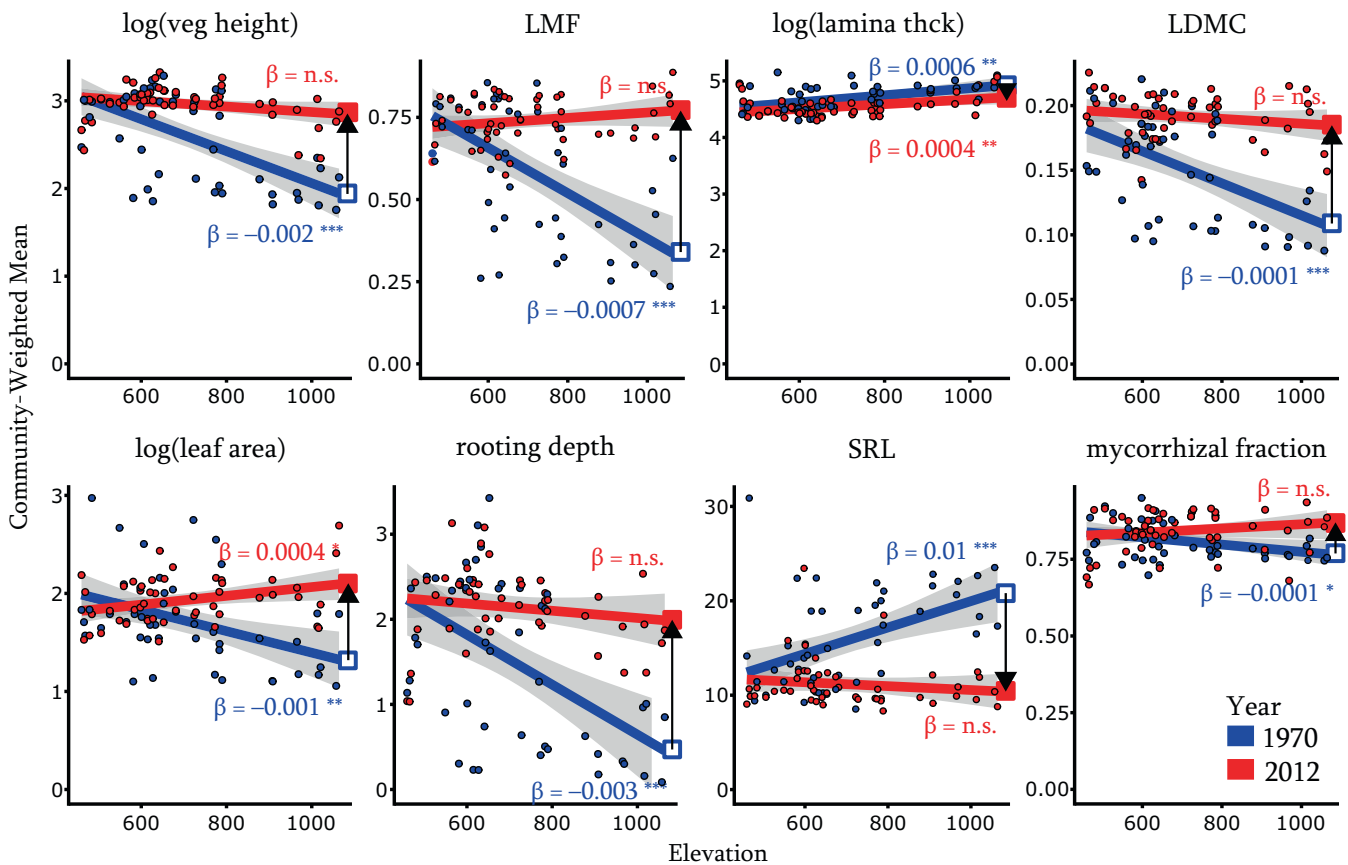
Panel B

FIGURE 1 (A) Change in community-weighted mean trait values with elevation for eight traits before (1970) and after global change (2012). 1970 = Blue; 2012 = Red. The slopes and significance of each regression are given. ns = $p > 0.05$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Regression slopes and intercepts for each year are given in Appendix S1: Table S6. For all eight traits, the slope became shallower or flat after warming and it even reversed for log leaf area. For rooting depth, ordinal categories were used. (B) Change in two functional diversity indices, functional richness and functional dispersion, before (1970) and after global change (2012). The diversity indices were calculated on the eight study traits. LDMC, leaf dry matter content; LMF, leaf mass fraction; SRL, specific root length.

elevational shift is context-dependent, with the models revealing a key role of trait–trait interactions. Generalized models containing only first-order effects show a negative effect of rooting depth on elevational shift (Appendix S1: Table S8, Models 3, 4, and 6). In contrast, models containing an interaction term between

rooting depth and either LMF or vegetative height have a positive main effect of rooting depth and an interaction term with a larger negative effect than the positive main effect of rooting depth (Appendix S1: Table S8, Models 1, 2, 5, 7, and 8). These interaction terms indicate that the association between shallow rooting depth and large
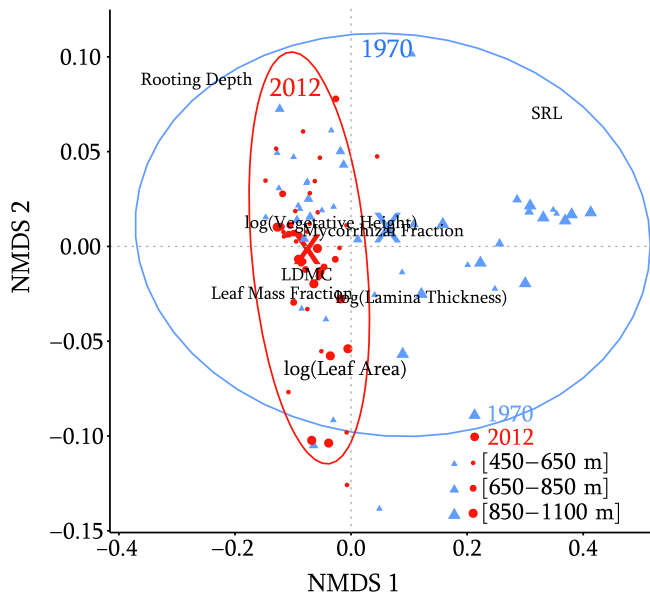
FIGURE 2 Changes in multivariate trait diversity of plots. Nonmetric multidimensional scaling (NMDS) ordination in two dimensions (stress = 0.076) of all plots in 1970 and 2012. Each data point represents a plot at a given time period. 1970 = Blue triangles; 2012 = Red circles. Ellipses give 95% CIs for each period. Icon size is proportional to plot elevation. LDMC, leaf dry matter content; SRL, specific root length.

elevational shifts occurs in species with high LMF or tall vegetative height (see illustration in Appendix S1: Figure S4). This contingency is illustrated in the regression tree in Figure 3B, where for those 21 species with LMF above 0.30, species rooted in the hummus layer (rooting depth ≤2) had the largest elevational shift. Thus, a species rooting depth is often but not always negatively associated with its elevational shift.

DISCUSSION

Overall, our results support four main conclusions: (1) Community-level trait changes over the 42-year period are largely consistent with those observed at the taxonomic level; (2) at both community and species levels, plant responses to environmental change largely occurred in seldom-measured traits, particularly root traits; (3) trait changes over the elevational gradient predicted trait changes over time; (4) trait changes were consistent with both the effects of warming and of nitrogen deposition.

Trait changes at the community and species levels

The trait composition, alpha diversity, and beta diversity of understory plant communities changed substantially
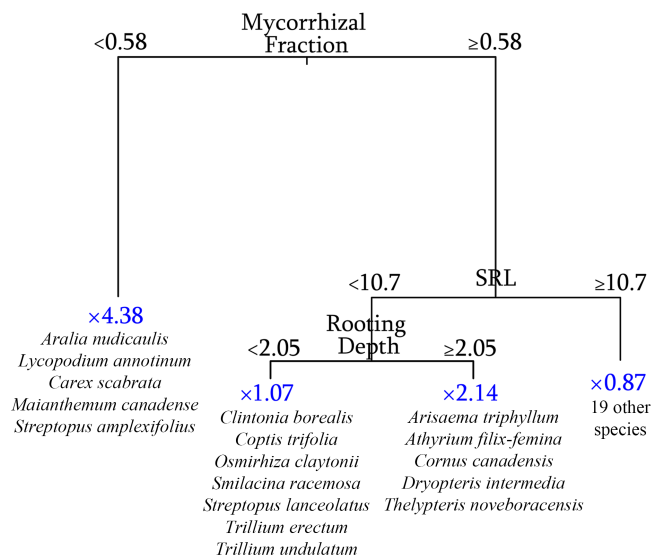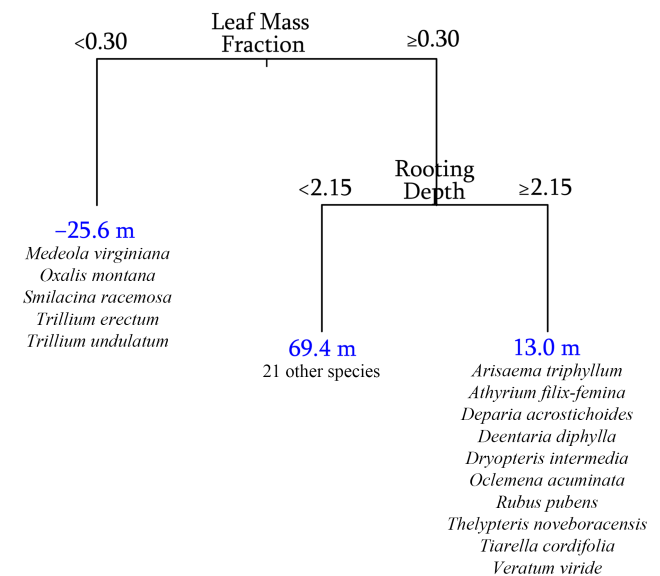

FIGURE 3 (A) Regression tree predicting change in species abundance as a function of traits. Traits at the forks give the predictor variables, with associated threshold values above each branch. Values in blue located at the branch tips give the predicted change in abundance. (B) Regression tree predicting change in elevation as a function of traits. Traits at the forks give the predictor variables, with associated threshold values above each branch. Values in blue located at the branch tips give the predicted change in elevation. Rooting depth of 2 or less includes roots in the top, middle, and bottom of hummus layer; greater than 2 indicates rooting at the hummus/mineral soil interface or deeper into the mineral soil.

over time, both within and among plots. As predicted, high-elevation communities gained low-elevation traits (i.e., those representatives of low-elevation communities in the 1970s), leading to shifts in mean trait values (Table 1, Prediction 1a). The strongest trends were in two

BOX 1 Comparison of trait–climate relationships at community and species scales over spatial and temporal gradients showing community-level spatial and temporal relationships are entirely consistent and changes in traits over time at the species and community levels are opposite for rooting depth and mycorrhizal fraction (abbreviations: LDMC, leaf dry matter content; LMF, leaf mass fraction; SRL, specific root length)

	Community scale	Species scale
Spatial gradient (at low elevation)	*Panel A* (see Figure 1A; Appendix S1: Table S6)	Not available
	↑ vegetative height	
	↑ LDMC	
	↑ leaf area	
	↑ LMF	
	↑ rooting depth	
	↓ SRL	
	↑ mycorrhizal fraction (weak)	
	↓ lamina thickness (weak)	
Temporal gradient (after 40 years)		
	Panel B	*Panel C*
	(see Figures 1 and 2; Appendix S1: Table S6)	(see Figures 3A and 3B; Appendix S1: Table S7)
	↑ vegetative height	
	↑ LDMC	**Shift in Elevation**
	↑ leaf area	↑ LMF
	↑ LMF	↓ rooting depth
	↑ rooting depth	
	↓ SRL	**Shift in Abundance**
	↑ mycorrhizal fraction (weak)	↓ mycorrhizal fraction
	↓ lamina thickness (weak)	

root traits: SRL decreased and rooting depth increased (Figure 2; Appendix S1: Table S3). Among-plot trait beta diversity (trait turnover) decreased over time, indicating trait homogenization (Table 1, Prediction 1c), and contemporary trait–elevation relationships became shallower than historical relationships (Figure 1A, Table 1, Prediction 1d; Appendix S1: Table S6). While the trait composition of low-elevation plots changed little, the composition of high-elevation plots shifted toward that of low-elevation plots (Figures 1 and 2). Functional richness generally increased over time, although high- and low-elevation plots changed in different ways (Table 1, Prediction 1b). These results—increased diversity, homogenization, and greater composition shifts at high elevation—mirror the taxonomic shifts reported by Savage and Vellend (2014) at this site. Previous meta-analyses of biodiversity change over time have focused largely on taxonomic diversity (Dornelas et al., 2013; Vellend et al., 2013), and at this site, trait diversity—thought to be more relevant to

ecosystem function—follows similar dynamics. Our findings differ from an observational study of temperate forests (Sonnier et al., 2014) but differ from modeling results of rainforest vine communities (Gallagher et al., 2013) and of temperate and boreal Atlantic forests (Thuiller et al., 2006). These contrasting findings suggest that the similarity of temporal changes in taxonomic and trait diversity may depend on the specifics of the study system and methods used.

To understand the differences in high- and low-elevation dynamics, we jointly examined four metrics reflecting community trait means and diversity. Functional dispersion and CWMs reflect species presence and abundance, but species richness (obtained from Savage & Vellend, 2014) and functional richness only reflect species presence. At low elevation, taxonomic and functional richness increased while functional dispersion and CWMs did not change. These patterns are consistent with new species, with novel

trait values arriving at low elevation but remaining at low abundance. To test this interpretation, we removed species from our analyses that were newly arrived at low elevation (absent in 1970, present in 2012), had low within-plot abundance, and had outlying trait values (7 of 36 species: *Maianthemum canadense, Carex intumescens, Phegopteris connectilis, Athyrium filix-femina, Circaea alpina, Thelypteris noveboracensis* and *Prenanthes altissima*). As expected, this curated dataset did not show an increase in functional richness in low-elevation plots between the two surveys (Appendix S1: Figure S5). At high elevation, taxonomic richness increased (Savage & Vellend, 2014) and CWMs shifted toward low-elevation trait values, but functional richness and dispersion did not systematically change. Together, these changes are consistent with a scenario where two types of responses occur simultaneously: a few new species arrived with trait values within the community's preexisting range, and those preexisting species with low-elevation trait values increased in relative abundance (see Appendix S1: Figure S6 for illustration). Overall, our results show that scarce species with outlying trait values can have a disproportionately large influence on community trait metrics (Katabuchi et al., 2017), and that considering the trait values and relative abundances of species by jointly considering a combination of community metrics helps draw a full portrait of complex community trait dynamics.

At the species level, three traits were moderate predictors of species abundance and elevation changes over time (Table 1, Prediction 2a). Species with high LMF and shallow rooting depths experienced large uphill shifts in elevation, and species less extensively associated with arbuscular mycorrhizae (AM) experienced large increases in abundance (Appendix S1: Table S7). As such, the results did not support the prediction that the same traits would predict species and community responses over time (Table 1, Prediction 2b; Box 1; Figure 3A). Contrasting patterns at the species and community level are consistent with other studies' finding that the traits underpinning the response of the most abundant species are not necessarily indicative of those determining the response of all species (Katabuchi et al., 2017). CWMs are most strongly influenced by the trait values of abundant species, while species-level analyses equally weight all species. These mismatches caution against carrying inferences across these biological scales (Ackerly et al., 2002, see also Kramer-Walter et al., 2016; Laughlin et al., 2018; Mitchell et al., 2018).

Seldom-measured traits are linked to plant response to global change

The strongest change in community composition occurred in two belowground traits: SRL and rooting depth.

Similarly, two of the three traits associated with species elevational and abundance responses were two root traits (rooting depth and mycorrhizal fraction). A different root trait, SRL, has been found to be associated with climatic gradients at the global scale (Freschet et al., 2017; Laughlin et al., 2021). These traits are seldom measured. Our measurements did include three of the most commonly measured traits (Kattge et al., 2020) that also define global trait dimensions (Diaz et al., 2016)—LMA, leaf area, and vegetative height—but these traits did not predict community- or species-level responses. The fact that LMF was associated with species uphill shifts suggests that biomass allocation captures the aspects of species ecology not reflected in traditional physio-morphological traits (Freschet et al., 2018; Umaña et al., 2021). Yet, allocation traits are not part of the set of classic traits (Pérez-Harguindeguy et al., 2013), nor of the set of traits expected to affect species responses to climate change (Aubin et al., 2016, 2018).

These results suggest that studies not measuring root or allocation traits (i.e., most studies to date) may thus be missing a key aspect of community response to global change and of efforts to link the plant phenotype to performance—a core goal of trait-based ecology (Shipley et al., 2016; Salguero-Gómez et al., 2018). Our results encourage future research to include root traits and biomass allocation traits to the set of routinely measured traits when monitoring trait responses of plant communities to environmental change.

Community-level trait relationships with spatial and temporal gradients are coherent

Our results show strong coherence in the community-level trait responses to spatial and temporal gradients (Table 1, Prediction 3). All temporal shifts in community-weighted trait means mirrored the historical (1970s) patterns of CWMs along the elevation gradient (Box 1, Panels A vs. B). Moreover, the relative strength of trait responses to spatial and temporal temperature gradients was similar: those traits with the strongest change along elevation also showed the largest change over time (rooting depth, SRL, LMF, and LDMC), while those traits with the weakest change with elevation also showed weak to no change over time (mycorrhizal fraction and lamina thickness). These results suggest that the environmental gradient(s) changing over space and time are the same. In our system, the temperature gradients are clear over both space and time. This is less obvious for nitrogen availability, given a decrease in nitrogen deposition rates between the two surveys. However, if nitrogen has accumulated in the soil over time, the temporal nitrogen gradient would then also mirror the spatial nutrient availability gradient from high

to low elevations. Regardless of the exact causes, these similarities give hope that the extensive literature on spatial environmental gradients can inform temporal responses of communities to global change.

Potential drivers of vegetation change

With any observational data, linking ecological change to specific drivers involves uncertainty. The shifts in individual traits we found at the community and species levels were partly consistent with findings from comparable studies on the effects of warming and fertilization, as developed in the *Introduction*. Also, changes in alpha and beta trait diversity were consistent with the expected effects of both warming and atmospheric depositions. Based on the contrast between elevational shifts in species distribution at Mont-Mégantic and the absence of such shifts at a comparable site with less pronounced warming, an earlier study at this site (Becker-Scarpitta et al., 2019) indicated warming as a key driver of vegetation change. Our results in this paper suggest the possibility of an influence of atmospheric nitrogen deposition as well.

Shifts in individual traits were more consistent with the direct effects of warming on plants, via increased temperatures and prolonged growing seasons, than with indirect effects via reduced water availability. Our findings are partly in line with studies on the direct effect of warming temperatures. Shifts in two traits were in the same direction as other studies on the direct effect of warming, and the shift in one trait was opposite. Our observed increase in leaf area and decrease in SRL were expected from warming, but the decrease in leaf thickness was not. In contrast, the increase in leaf area is opposite to our expectation from water limitation. Similarly, the directions of trait shifts were only partly consistent with the effects of fertilization (i.e., nitrogen addition) reported in the literature: the increase in leaf area was consistent with expectations, and the increase in LDMC and decrease in SRL were not.

We cannot assess whether our findings on rooting depth and mycorrhizal associations are consistent with the literature because those two traits showed shifts in opposite directions at the species and community levels. Last, the increase in maximum vegetative height is consistent with both a direct effect of warming and an effect of atmospheric deposition. While increased height has been reported in response to warming, both in temperate understories (Amatangelo et al., 2014; Blondeel et al., 2020; Diekmann & Falkengren-Grerup, 2002) and in other systems (Brown & Zinnert, 2021; Moles et al., 2014; Swenson & Weiser, 2010), it has also previously been

reported to increase in response to soil fertility in temperature understories (Amatangelo et al., 2014; Blondeel et al., 2020; Diekmann & Falkengren-Grerup, 2002; Maes et al., 2020; Perring et al., 2018) and in other systems (Brown & Zinnert, 2021; Moles et al., 2014; Swenson & Weiser, 2010).

Although results from studies conducted in other systems (e.g., grasslands, tropical or temperate trees) or at other scales (e.g., global) provide only a limited basis for making predictions about our results for temperate understory perennials, overall, the fact that fewer than half the trait shifts were consistent with expectations from warming or from atmospheric nitrogen deposition suggests that both factors may have had some influence. As discussed in the *Introduction*, the theoretical expectations of the effects of warming and atmospheric deposition on alpha and beta diversity can be similar such that our findings for trait diversity within and among communities can also be consistent with both.

In sum, our study found changes in plant traits consistent with those observed at the taxonomic level, a critical importance of root and allocation traits in mediating responses to global change, and a set of community- and species-level changes likely driven by both climate warming and atmospheric deposition.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Trait data (Messier, 2019) are available in Zenodo at https://doi.org/10.5281/zenodo.3258342. Census data (Savage & Vellend, 2014) are available at https://www.ecography.org/appendix/ecog-01131.

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SUPPORTING INFORMATION

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