

Contrasting plant responses to multivariate environmental variations among species with divergent elevation shifts

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Abstract. The general predictions of climate impacts on species shifts (e.g., upward shift) cannot directly inform local species conservation, because local-scale studies find divergent patterns instead of a general one. For example, our previous study found three shift patterns with elevation (strong down-, moderate down-, and up-slope shifts) in temperate mountain forests. The divergent shifts are hypothesized to arise from both multivariate environmental variations with elevation and corresponding species-specific responses. To test this hypothesis, we sampled soils and leaves to measure elevation variations in soil conditions and determined plant responses using discriminations against heavier isotopes, carbon (¹³C) and nitrogen (¹⁵N). Functional traits of the species studied were also extracted from a public trait dataset. We found that: (1) With low soil water contents at low elevations, only the leaves of up-shifters had lower ¹³C discriminations at low vs. high elevations; (2) With low soil P contents at high elevations, only the leaves of moderate down-shifters had higher ¹⁵N discriminations at high vs. low elevations; (3) The leaves of strong down-shifters did not show significant elevation patterns of the discriminations; (4) The contrasting responses among the three types of shifters agree with their functional dissimilarity, suggested by their separate locations in a multitrait space. Taken together, the divergent shifts are associated with the elevation variations in environmental conditions and contrasting plant responses. The contrasting responses could result from the functional dissimilarity among species. Therefore, a detailed understanding of both local environmental variations and species-specific responses can facilitate accurate predictions of species shifts to inform local species conservation.

Key words: climate change; functional trait; land-use change; nutrient; species shift; stable isotope; water.

INTRODUCTION

Some biogeographical studies showed general patterns of species range shift (upward and poleward shift) associated with warming temperatures (Parmesan and Yohe 2003, Lenoir and Svenning 2015), but other studies have highlighted that temperature is only related to range limits of no more than one-third of species studied (Normand et al. 2009) and even weakly related to observed range limit shifts in Rumpf et al. (2019). Moreover, local studies observed shifts of different directions and rates, e.g., multiple shift patterns with elevation (Guo and Lenoir 2018). Our previous study also showed divergent

shift patterns across woody species along the same elevation gradient (Zhang et al. 2019). In that study, we found some oak species moved down-slope as forest recovered from disturbance, despite warming temperatures. Therefore, the divergent shift patterns at local scale could be driven by other factors in addition to temperature, and understanding of these potential factors is a crucial knowledge gap in the study of species shifts under changing climate.

The divergent shift patterns could result from multivariate nature of a changing environment (Kling et al. 2020), including nutrient and water. Nutrient limitation is a fundamental limitation of primary producers (Elser et al. 2007, Vitousek et al. 2010), therefore fertilization is used to mitigate effects of nutrient limitation on forest growth, e.g., pine plantation (Zhai et al. 2015). However, nutrient limitation has not received sufficient attention

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regarding its impacts on species shifts (Fajardo and Piper 2017). Nutrient limitation is potentially important, because plant nutrient status could determine both plant responses to changing climate, e.g., drought (Gessler and Schaub 2017), and predictions of species distributions (Buri et al. 2017). The variation in nutrient distribution can be found along elevation gradients in mountains, e.g., soil nutrient contents could be lower at higher elevations (Wang 2018). Therefore, decreasing foliar nutrient contents (foliar %N and %P) with elevation have been found in some studies, e.g., Asner (2017), but this elevation pattern cannot be applied globally (Körner 2007). The low nutrient availability at high elevations further constrains plant growth in Alpine ecosystems where there are early-successional soils (Hagedorn and Gavazov 2019). Moreover, drought-driven forest shifts were widely observed (Fei et al. 2017). In mountain systems, moisture availability can mediate warming-caused up-slope shifts of treeline (Sigdel et al. 2018). Water availability could be reduced at lower elevations (Normand et al. 2009), and variation in water availability account for plant shifts in the mountains of California, USA (Rapacciuolo 2014). In temperate mountain forests of our study areas, the water availability at low elevations might be reduced under a warming climate and consistent rainfall pattern (Zhang et al. 2019). Therefore, the reduced water availability was hypothesized to lead to up-slope shifts of some woody species (Fig. 1). Down-slope shifts of the other woody species are hypothesized to arise from lowland forest recovery with more growth space available following cessation of historical harvests, particularly when nutrients are

limiting at high elevations (Fig. 1). Although these hypothesized impacts of nutrient, water, and growth space might agree with the field conditions in our study area, there is a lack of rigorous hypothesis tests, leading to a limited understanding of the impacts of multivariate environment on plant elevation shifts.

Plant responses to the elevation changes in water and nutrient conditions can be determined by discrimination against heavier carbon (^{13}C) and nitrogen (^{15}N) isotopes, respectively, from their sources to leaf materials in conjunction with other measurements (e.g., foliar nutrient contents and soil isotope signatures). Atmospheric CO_2 diffuses into air-filled spaces within leaves and is fixed by photosynthesis, and both the diffusion and biochemical processes discriminate against ^{13}C in favor of ^{12}C . The discrimination against ^{13}C within leaves declines with increasing water stress, because it reduces atmospheric CO_2 diffusion into leaves by closing stomata. Then, a greater proportion of $^{13}\text{CO}_2$ within leaves is fixed during photosynthesis (Farquhar and Sharkey 1982). Therefore, lower ^{13}C discrimination is observed as a plant experiences more limited water availability, e.g., at low elevations (Lajtha and Getz 1993). Similarly, plant nitrogen uptake discriminates against ^{15}N in favor of ^{14}N , and the discrimination increases with lower plant N demand or root growth/activity (Fry et al. 2000, Robinson et al. 2000). The low N demand could arise from plant P limitation based on optimum N:P ratios for plant growth (Ågren and Wetterstedt 2012). Therefore, higher ^{15}N discrimination is observed as plant response to a more limited P availability (Inglett et al. 2007, Zhai et al. 2018). Together, our study measured

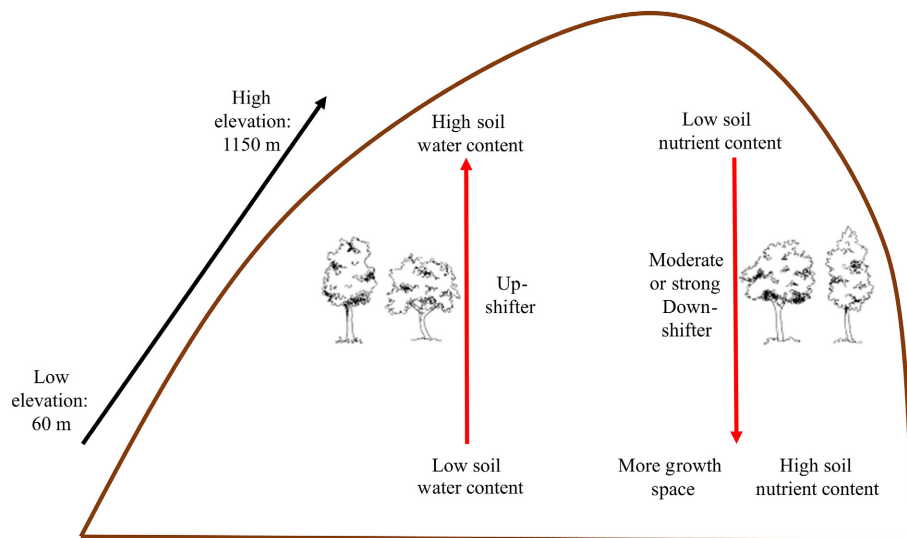


FIG. 1. Conceptual figure of the elevation patterns (from 60 to 1,150 m) of environmental conditions (soil water and nutrient contents and growth space) and the associated species shift patterns. The elevation change in soil water is hypothesized to drive up-slope shifts, and the elevation changes in soil nutrient and lowland growth space are hypothesized to drive down-slope shifts. Note: Seed-related processes (seed dispersal and germination) and parent tree effect were also considered in this study to understand the shift patterns.

the ^{13}C and ^{15}N discriminations to indicate plant responses to the elevation changes in soil water and nutrient contents, respectively.

The divergent shift patterns could also arise from different responses to environmental changes among species (Kling et al. 2020), and the different responses could be caused by species-specific functional traits, affecting plant growth with changing environment (Violle et al. 2007). For example, plant responses to water and nutrient limitations can be defined by leaf thickness (LT) and specific leaf area (SLA) (Griffin-Nolan 2018, He et al. 2018), and leaf dry matter content (LDMC) and leaf size (Hodgson 2011), respectively. Based on these functional traits, species showed different probabilities of colonizing different elevations (Matteodo et al. 2013). Therefore, species with divergent shift patterns may arise from their functional dissimilarities, determined by a multivariate analysis of functional traits (Stahl et al. 2013). The functional dissimilarities can be visualized by separate locations of species in a multidimensional space, defined by plant functional traits. To test the functional dissimilarities, our study extracted functional trait data of the species studied from open-access plant trait databases. These public data have been widely used similarly by other studies quantifying functional attributes of local species, e.g., quantifying functional diversity (Ouyang 2019).

To test if the divergent shift patterns were attributed to the multivariate environmental variations and species-specific plant responses, we measured the elevation variations in soil conditions (soil water and nutrient contents), and we also determined the plant isotope responses with leaf samples from eight woody species characterized with divergent shift patterns (strong down-, moderate down- and up-shifters). Furthermore, to understand the species-specific responses, we evaluated the functional dissimilarities among the species studies using their functional traits from a trait database. In detail, we tested the following hypotheses: (1) Soil water content increases with elevation, but soil nutrient contents decrease with elevation; (2) The ^{13}C discrimination of up-shifters and ^{15}N discrimination of down-shifters increases with elevation; (3) Strong down-shifters have higher growth rates than moderate ones; (4) There are functional dissimilarities among the three types of shifters.

MATERIALS AND METHODS

Study area

The study area was located in mountain forests in Liu'An of Anhui province, eastern China ($115^{\circ}22'–116^{\circ}11'E$ longitude and $31^{\circ}06'–31^{\circ}48'N$ latitude). Based on monthly climate records between 1996 and 2014, this area receives a minimum 28.6 ± 1.1 mm, maximum 253.3 ± 88.5 mm, and average 90.8 ± 77.9 mm precipitation, and a minimum $2.7 \pm 1.3^{\circ}\text{C}$, maximum $30.8 \pm 7.0^{\circ}\text{C}$, and average $16.4 \pm 8.8^{\circ}\text{C}$. From 1996 to 2014, the

mean temperature for the study area increased gradually from 16.0°C to 17.7°C , but no significant change in precipitation has been recorded in this area from 1996 to 2014 (Zhang et al. 2019).

There were 89 permanent forest plots (25.82×25.82 m) established at regularly spaced sites along an elevation gradient from 60 to 1,150 m. Before 1970, this area was harvested for timber and fuel woods. The lowland plots suffered more from the harvests (i.e., a higher number of stems harvested) compared with ones located at higher elevations, but the harvest and natural disturbances (e.g., fire) have been strictly limited by local government agencies since 1970, and this conservation policy contributed to the natural forest recovery in our study site (Zhang et al. 2019). Beginning in 1989 and every five years through 2009 (1989, 1994, 1999, 2004, and 2009), in total 3,316 living woody stems ≥ 5 cm in diameter at breast height (DBH) of 18 woody species were tagged, measured (DBH), recorded according to growth status (live or dead) and identified to species level.

Sample collection and measurements

Woody species.—In our study site (i.e., Liu'An), the species shift directions and rates were quantified by changes in species mean elevations, that is the mean elevation weighted by the number of individuals per elevation in each census. The calculation details can be found in Zhang et al. (2019). We sampled eight woody species, showing three shift patterns: (1) Strong down-shifters (shift rate < -5 m/yr): *Dalbergia hupeana*, *Cerasus pseudocerasus*, and *Quercus glauca*; (2) Moderate down-shifters (-5 m/yr \leq shift rate ≤ 0 m/yr): *Pinus massoniana*, *Lindera glauca*, and *Cunninghamia lanceolata*; (3) Up-shifters (shift rate > 0 m/yr): *Pinus taiwanensis* and *Liquidambar formosana*. The eight species are dominant ones, collectively representing $>80\%$ of the individuals in our study site. In addition to this study site (Liu'An), our previous study reported the different shift patterns among species with data from Liu'An and the other four study sites in the same region (Zhang et al. 2019). This study aimed to investigate mechanisms of the different shift patterns among species along the same elevation gradient.

Plots.—In September 2016, we collected samples in 16 plots from the 89 plots established in 1989. These plots were uniformly distributed along the same slope from 310 to 1,150 m, leading to one plot per 52 m with elevation (Appendix S1: Fig. S1). Moreover, these plots were set up with similar aspects to control the effects of aspect. In each sampling plot, we chose three random subplots (5×5 m), which lay along a diagonal line crossing the sampling plot. In each subplot, two soil samples were collected from the surface soil (0–20 cm) and subsurface soil (20–40 cm) (after forest floor litter was removed). Soil samples were sealed by preservative film and cellulose tape and individually stored in plastic zip bags to avoid evaporation. In addition, in each sampling

plot, ≥ 10 fully expanded and sun-exposed leaves were sampled from the upper canopy of an individual stem, and three stems were chosen for each of the eight selected species. The leaf samples were individually stored in plastic bags wrapped with wet gauze. These samples were collected by a single team of researchers using standardized collection protocols.

Measurements of soil and plant leaves.—To measure gravimetric soil moisture, we removed stones and roots in the soil core sample by sieving through a coarse sieve. Then, we calculated soil moisture by the difference between fresh and dry mass (dried at 105°C until a constant mass), and the difference was standardized with dry mass. Remaining soil samples were air-dried (at ~15°C), sieved (2 mm mesh), and stored in air-tight plastic bags to measure: (1) soil total nitrogen (TN, g/kg) by an elemental analyzer (Vario EL III, Elementar, Germany); (2) total phosphorus (TP, g/kg) using a UV-visible light spectrophotometer.

Foliar and soil samples were oven dried (60°C for at least 48 h) and ground. We loaded both soil and foliar samples (≥ 5 mg) into individual tin cups to measure N content (%N) and stable isotope ratios. The stable isotope measurements were made by a continuous flow isotope ratio mass spectrometer (Costech Analytical Technologies, USA) at the isotope analysis laboratory, Nanjing Forestry University. The stable isotope ratios of carbon and nitrogen were reported using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, applying Eq. 1:

$$\delta^y\text{X} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \cdot 1,000\text{‰} \quad (1)$$

The isotope discriminations against ^{13}C and ^{15}N relative to their respective sources (atmospheric CO_2 and soil N) were calculated using Eq. 2:

$$\Delta^y\text{X} = (\delta^y\text{X}_{\text{source}} - \delta^y\text{X}_{\text{leaf}}) / \left(1 + \frac{\delta^y\text{X}_{\text{leaf}}}{1,000} \right) \quad (2)$$

where y is the atomic mass of the heavy isotope (C: 13 and N: 15), X is the atom of interest (C and N), and R_{sample} R_{standard} are the measured ratios of the sample and a reference standard. $\delta^{13}\text{C}$ values are expressed relative to the Vienna Belemnite of the Pee Dee formation and $\delta^{15}\text{N}$ values are expressed relative to standard air nitrogen. $\delta^y\text{X}_{\text{source}}$ is the isotope ratio of sources, and $\delta^y\text{X}_{\text{leaf}}$ is the isotope ratio of leaves. The $\delta^{13}\text{C}$ of atmospheric CO_2 of our study site (-8.31‰) was extracted from nearby stations affiliated to the World Data Centre for Greenhouse Gases, World Meteorological Organization (WMO) (<https://gaw.kishou.go.jp/>). The elevation pattern of $\delta^{13}\text{C}$ of atmospheric CO_2 was assumed to be constant in our study and others, e.g., Wu et al. (2017), because it had a marginal effect on foliar $\delta^{13}\text{C}$ (Körner and Farquhar 1988). There was a steady decrease in the atmospheric CO_2 partial pressure at a rate of 9.5% per

1,000 m elevation (McElwain 2004), but the decreasing partial pressures only caused minor changes in the ^{13}C discrimination. For example, the effect of CO_2 partial pressure was greatest in the plots at the highest elevation where the discrimination was only reduced by less than 10% of the original value (Seibt et al. 2008). Moreover, at the same elevation, different species are exposed to the same CO_2 partial pressure. Together, we assumed that CO_2 partial pressure does not affect our comparison among the species studied. For soil samples, we measured the $\delta^{15}\text{N}$ of N content.

Functional traits

From the 18 woody species in our study area, functional trait data were extracted based on 11 species: (1) strong down-shifters: *Quercus chenii*, *Q. glauca*, *D. hupeana*, and *Pistacia chinensis*; (2) moderate down-shifters: *P. massoniana*, *Cunninghamia lanceolata*, *L. glauca*, and *Diospyros lotus*; and (3) up-shifters: *L. formosana*, *Litsea cubeba*, and *L. glauca*. The species selection was based on data availability from the TRY plant trait database (Kattge 2020). Our functional trait analysis was based on the following functional traits: SLA, leaf area (LA), leaf phenology (LP), LT, LDMC, seed dry mass (SDM), and maximum height (HT). For each of these traits, the mean value of one species was calculated by all observations found from the trait database. The maximum heights were compiled from Wu and Raven (1999). Additionally, the growth rate of basal area (BA.Growth) was added to the functional trait analysis. BA.Growth was calculated by mean growth rate across the measured individuals from 1989 to 2009. Moreover, the BA.Growth was standardized with initial BA, as a way to account for the effects of tree size associated with differences in elevation-related productivity and tree age. The calculation details can be found in Zhang et al. (2019). To summarize the information above, we made a table to describe details of the data used for the functional trait analysis, including species name, shift group, functional traits, etc. (Appendix S1: Table S1).

Statistical analysis

Elevation patterns of soil and foliar attributes.—Both of the elevation patterns of soil (water content and N:P) and foliar (^{13}C and ^{15}N discriminations) attributes were analyzed by generalized least squares (GLS) and linear mixed-effects (LME) models, respectively (Appendix S1: Section S1). The residual structures of these models may vary by different dependent variables to allow for the spatial correlation with elevation and the heterogeneity in model residuals (Appendix S1: Section S1). Akaike information criterion was used to select models with different structures of the fixed effects and model residuals. Maximum likelihood was used to compare models with different fixed-effects structures (e.g., with or without the interactions of soil depth and elevation in the models

of soil attributes). Restricted maximum likelihood was used to compare models with different residual structures and estimate model parameters. We removed influential points and outliers (<5% total observations) identified by Cook's distance and standardized residuals, respectively. The violations of linearity, equal variance, normality, and independence (i.e. spatial independence with elevation) were examined by the residual plots along the fixed-effects factors and fitted values, the normal quantile plot, and the variogram of standardized residuals, respectively. The above statistical analyses were implemented in the R program (R Core Team 2020) and the *nlme* package (Pinheiro et al. 2019).

Relationship between foliar ^{15}N discriminations and foliar nitrogen content.—This relationship was calculated using Model II regression, because both foliar ^{15}N discriminations and foliar nitrogen content were measured values with random error (Sokal and Rohlf 1995). As the distributions of these two variables were not bivariate normal and their relationship was linear, Model II regression was calculated using the ordinary least squares method (Legendre and Legendre 1998). Foliar nitrogen content on the base-10 logarithmic scale was used in the analysis. The above statistical analysis was implemented using R and the *lmodel2* package (Legendre and Oksanen 2018).

Functional trait analysis.—Functional traits were analyzed with a multivariate analysis using non-metric multidimensional scaling (NMDS). NMDS was performed on a matrix of Euclidean distances among the nine species. Two dimensions were used in the NMDS, as adding more dimensions did not significantly reduce the stress value. The stress value of the NMDS was 0.06. The above statistical analysis was implemented in R and the *vegan* package (Oksanen 2020).

RESULTS

Soil water content and ^{13}C discrimination

There were lower soil water contents at low vs. high elevations (Fig. 2a, $P < 0.01$). With the low soil water contents at low elevations, there were no significant elevation patterns of ^{13}C discrimination for the strong (Fig. 2b) and moderate down-shifters (Fig. 2c). However, the up-shifters had lower ^{13}C discrimination at low vs. high elevations (Fig. 2d), suggesting their significant response to the lowland water limitation.

Soil N:P, ^{15}N discrimination, and foliar nitrogen

Soil N:P ratios increased with elevation (Fig. 3a), suggesting high P limitations at high elevations. With high P limitations at high elevations, neither the strong down-shifters (Fig. 3b) nor up-shifters (Fig. 3d) showed a significant elevation pattern for the ^{15}N discrimination. However, the moderate down-shifters had greater ^{15}N

discrimination at high vs. low elevations (Fig. 3c), indicating their significant nutrient response. Furthermore, the significant nutrient response of moderate down-shifters was suggested by their greater ^{15}N discriminations with lower foliar %N, i.e., the negative correlation in Fig. 4a.

Plant functional traits

The two-dimensional space was downscaled from the multidimensional space built by the functional traits (Fig. 5). Axis 1 was positively related to SLA, but negatively related to LT, LP (from deciduous to evergreen species), and BA.Growth. The second axis was positively related to LDMC and SDM, but negatively related to LA and HT. In this trait space, the species showing divergent shift patterns were grouped separately. Among the three shifter groups, the up-shifters had the highest LA and SLA (axis 1), the strong down-shifters had the highest LDMC and SDM (axis 2), and the moderate down-shifters had the highest BA.Growth (axis 1), greatest HT (axis 2), and were most dominated by evergreen species (axis 1) (Fig. 5).

DISCUSSION

Up-slope shifts are associated with low soil water contents at the low elevations

Only the up-shifters showed significantly lower ^{13}C discriminations at the low vs. high elevations. The isotope response aligns with the low soil water content at the low elevations in our study area. Other factors may confound the ability of ^{13}C discrimination to estimate the plant response to soil water variation with elevation, such as temperature-related changes in leaf traits (Vitousek and Field 1990, Maxwell and Silva 2018), but these changes contributed to higher ^{13}C discrimination at low vs. high elevations, which is opposite to our results. Therefore, these confounding influences tend to be offset by lowland water limitation (Van de Water and Leavitt 2002), leading to declining ^{13}C discriminations at low elevations, e.g., Li et al. (2009), which were also observed from the up-shifters in our study. The other confounding factor is the anisohydric degree of these species. Although direct measurements of anisohydric degree are not possible, we compiled published studies in Appendix S1: Table S2, suggesting that most of the species studied reduce stomatal conductance or ^{13}C discrimination under limited water availability. Therefore, there are minimal anisohydric effects on the species studied, and water availability limitation provided an important constraint on the lower ends of plant distribution (Colwell et al. 2008, Rigling 2013), but only for the up-shifters in our study.

Moderate down-slope shifts are associated with low soil nutrient contents at the high elevations

The significantly increasing soil N:P ratios with elevation in our study area suggested P limitation of the high

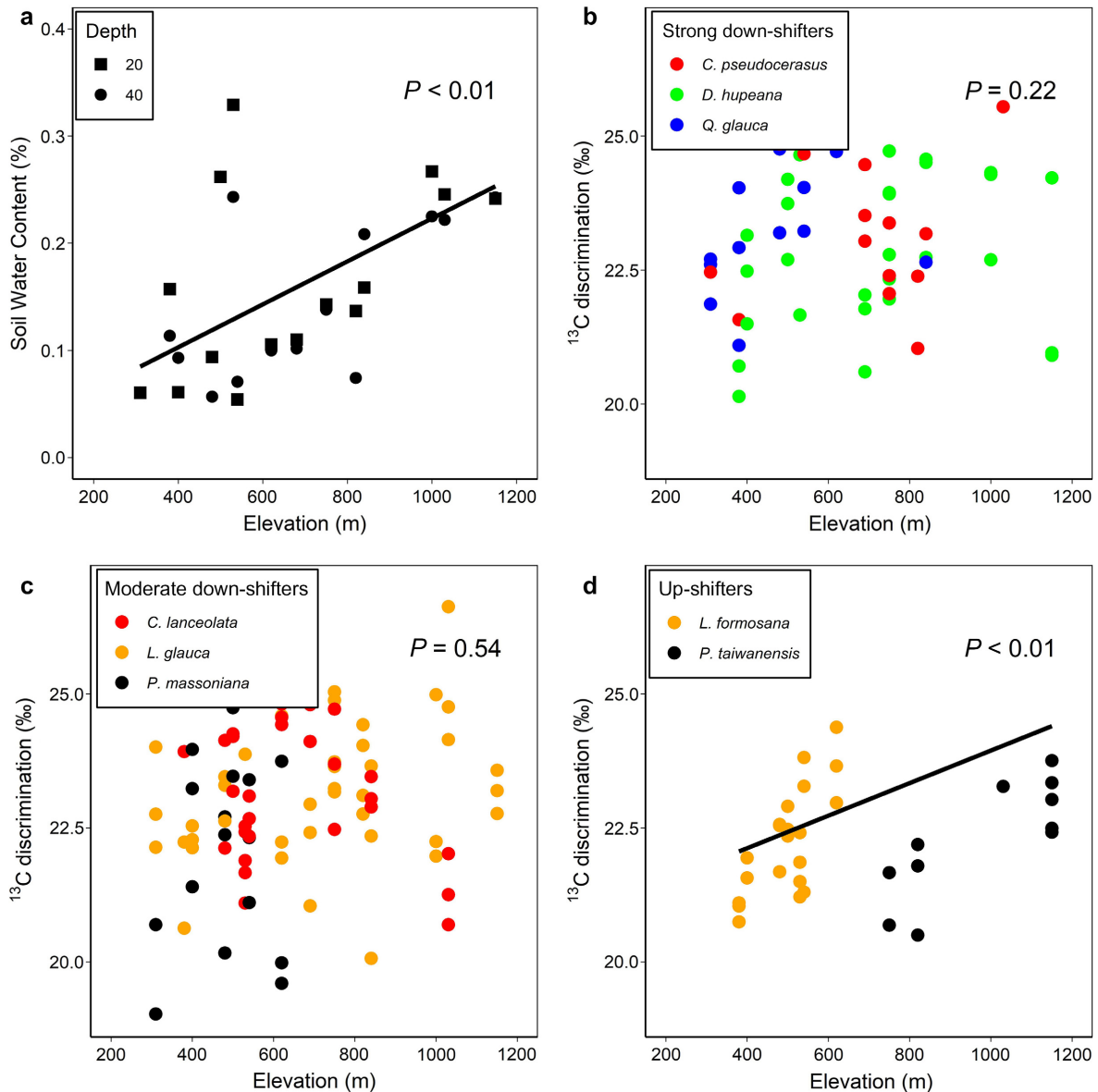


FIG. 2. The relationships between elevation (m) and (a) soil water content; (b) ^{13}C discrimination from air to leaf of the strong down-shifters; (c) ^{13}C discrimination from air to leaf of the moderate down-shifters; and (d) ^{13}C discrimination from air to leaf of the up-shifters. The relationships of elevation with soil water content and ^{13}C discrimination are denoted by the fitted lines based on the population means of the Eqs. 1 and 2 from Appendix S1: Section S1, respectively. The solid lines denote significant elevation effects at a significance level of 0.05. The significances of the elevation effect are denoted by the P -values based on the above equations. One point in the figures is one measurement of an individual sample, and its color is coded by genera.

elevations (Elser et al. 2010). P limitation could be related to faster N deposition (Lovett and Kinsman 1990) or different mineralization rates between N and P (Wang et al. 2018) at high elevations. Importantly, P limitation could reduce plant N demand contributing to lower N uptake, further increasing ^{15}N discriminations. Additionally, the lower N uptake and resultant discrimination may arise from reduced root activity, due to the decreasing water viscosity and cell membrane permeability in a cold climate characterizing high elevations (Mayor 2017). The higher

discrimination with lower N uptake is further suggested, as foliar %N declined with higher discrimination in our study and others, e.g., Brookshire et al. (2020). Potential confounding factors on ^{15}N discrimination is a switch of plant N source from inorganic to organic forms of N by declining temperature with elevation (Schimel and Bennett 2004), but the switch may lead to lower discriminations (Averill and Finzi 2011), instead of the higher discrimination found in our study. Therefore, the confounding effects are marginal on the species comparisons in our study.

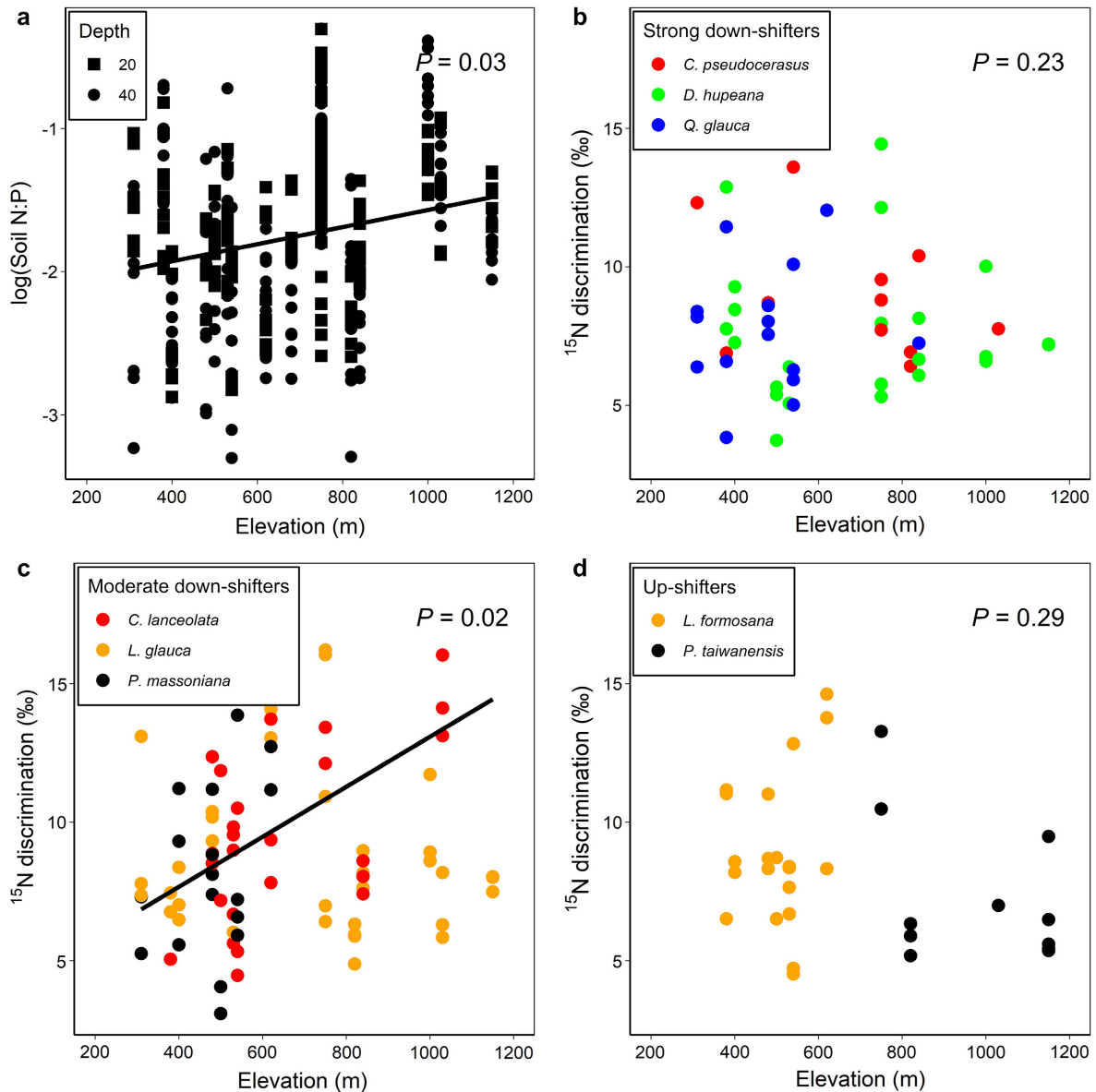


FIG. 3. The relationships between elevation (m) and (a) natural logarithm of soil nitrogen and phosphorus ratio; (b) ^{15}N discrimination from soil to leaf of the strong down-shifters; (c) ^{15}N discrimination from soil to leaf of the moderate down-shifters; and (d) ^{15}N discrimination from soil to leaf of the up-shifters. The relationships of elevation with soil N:P and ^{15}N discrimination are denoted by the fitted lines based on the population means of Eqs. 3 and 4, respectively, reported in Appendix S1: Section S1. The solid lines denote significant elevation effects at a significance level of 0.05. The significances of the elevation effect are denoted by the P -values based on the above equations. One point in the figures is one measurement of an individual sample, and its color is coded by genera.

As P limitation can constrain plant growth by decreasing investments in P-rich RNA required for organismal growth (Elser et al. 2010), it constrained the up-slope shifts of responsive species, i.e., the moderate down-slope shifting species in our study. Notably, highland nutrient stress varies among distantly geographical regions, e.g., highland P limitation in northeastern China (Zhao et al. 2016), but N limitation in the Peruvian Andes (Fisher et al. 2013). These highland nutrient

limitations are further supported by field experiments in which fertilization stimulated highland forest growth (Möhl 2019). Therefore, highland nutrient limitation could determine upper limits to plant distributions (Rehm and Feeley 2015). In our study, with the limited potential of up-slope shifts by the highland nutrient stress, species may leverage the lowland growth space available from the cessation of historical harvests, contributing to their down-slope shifts.

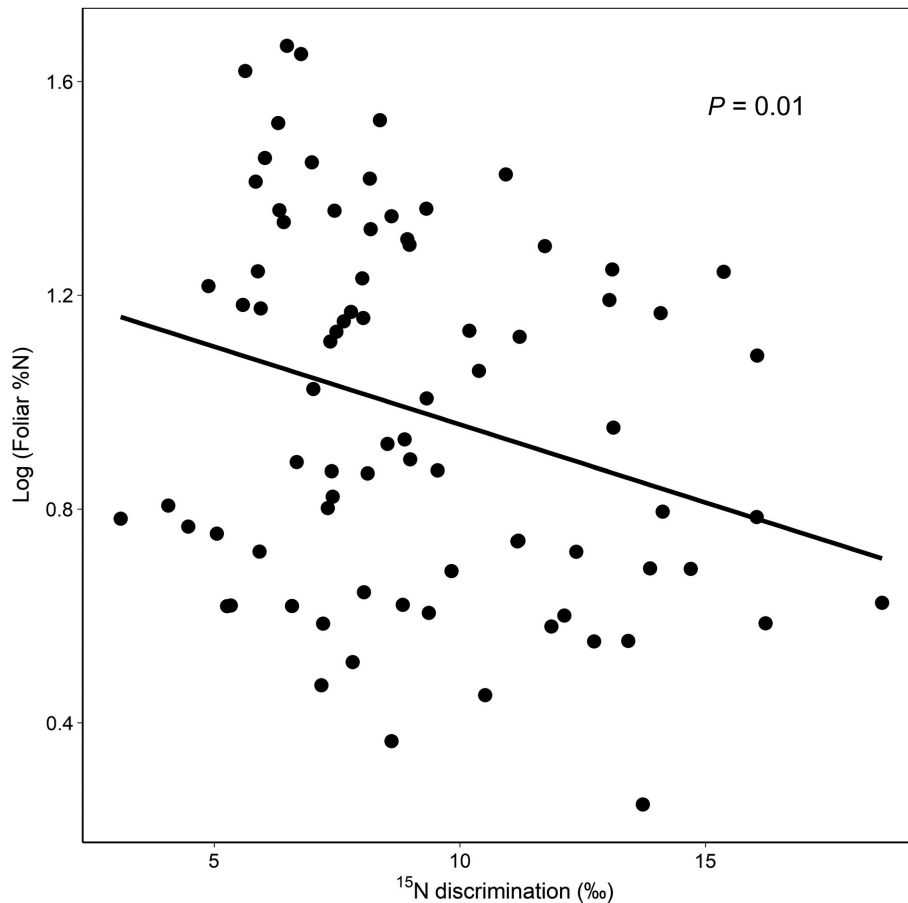


FIG. 4. The relationships of the moderate down-shifters between the foliar ^{15}N discrimination and foliar nitrogen content at the base-10 logarithmic scale. The relationship is denoted by the fitted line that was based on the linear II regression analysis. The significance of the relationship is denoted by the P -value. One point in the figures is one measurement of an individual sample.

Three types of shifters were grouped separately in the trait space

Compared with the up-shifters and moderate down-shifters, the strong down-shifters did not show the significant isotope responses with elevation. This finding might suggest their tolerance to the variations in soil water and nutrient with elevation. Notably, compared with the other shifters, the tolerances of strong down-shifters to the lowland water and high nutrient limitation were also supported by their relatively low SLA and high LDMC, respectively (Peirez-Harguindeguy 2013). With the tolerances, the strong down-shifters could take advantage of the lowland growth space following the cessation of historical harvests in our study site (Zhang et al. 2019), and the harvest cessation-caused down-slope shifts of forests are also found in the mountains of the northeastern USA (Wason and Dovciak 2017). Therefore, post-harvest regeneration or land-use history should be considered to predict plant-distribution shifts (Miller and McGill 2018, Wang et al. 2019). Compared with strong down-shifters, the moderate down-shifters

had faster growth rates. Therefore, instead of growth rate, other mechanisms could explain their differences in the shift rate. One mechanism might be related to seed-related processes, including seed dispersal and germination. A long dispersal can facilitate elevation shifts and space colonization (Cannone and Pignatti 2014), characterizing the dominant species of strong down-shifters, e.g., oak species (*Q. chenii*, *Q. glauca*) (Johnson and Shifley 2009). Dispersal distance tends to be negatively related to plant height (LaRue and Holland 2018), therefore the shorter heights of strong down-shifters could contribute to their long dispersal compared with the moderate down-shifters. Moreover, seed germination initiates plant establishment, potentially affecting plant shifts. Seed germination is positively affected by SDM (e.g., Stanton 1984) which was higher on the strong down-shifters compared with moderate ones.

The three types of shifters were grouped separately in the trait space. Axis 1 of the space is related to traits more responsive to water stress, such as LT and SLA. A similar dimension is also found in another study analyzing intraspecific trait variations as they change with

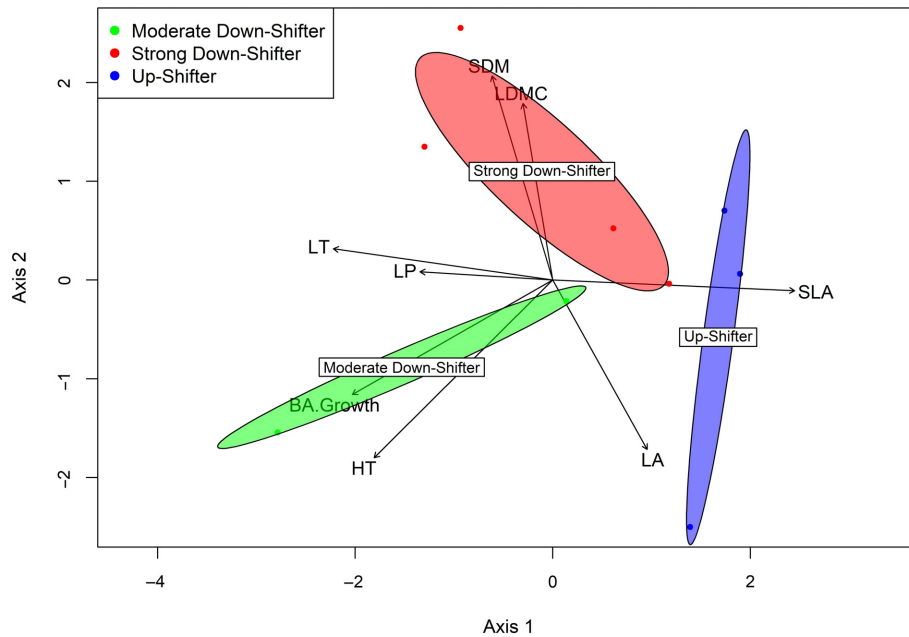


FIG. 5. Two-dimensional NMDS ordination diagram with the three groups of shifters (including strong down-shifters, moderate down-shifters, and up-shifters) and three ellipses showing the 0.95 confidence regions for the locations of group centroids. BA.Growth, growth rate of the basal area; HT, maximum tree height; LA, leaf area; LDMC, leaf dry matter content; LP, leaf phenology; LT, leaf thickness; SDM, seed dry mass; SLA, specific leaf area.

elevation (Umaña and Swenson 2019). The other axis is related to traits more responsive to nutrient stress, such as LDMC (Hodgson et al. 2011). In the trait space, the separate locations of these species groups suggested that their functional dissimilarities may account for the divergent shift patterns among species along the same elevation gradient. For example, based on the dissimilarity in leaf traits suggesting tolerance to water stress (e.g., SLA, LT, LA), the down-shifters showed higher tolerance than the up-shifters, and the tolerance differences aligned with the lower soil water content in low elevations compared with high ones. Therefore, the general shift patterns (e.g., upward shift) with warming climate could be mediated by species-specific plant responses to environmental variations. These species-specific responses have also been found in other elevation-based studies. For example, water stress has stronger effects on highland vs. lowland species from the Bavarian Alps in Germany (Rosbakh et al. 2017). In addition to the functional differences, the different shift patterns might be related to remaining trees after the harvest was ceased, particularly for the species of strong down-shifters in the low elevations, because these trees could be parent trees contributing to the downshift. However, the species of strong down-shifters made up a small percentage of trees in the low elevations in the beginning, based on the survey data in 1989 (Appendix S1: Table S3). Therefore, the parent tree effect cannot be supported by the forest survey data.

CONCLUSION AND MANAGEMENT IMPLICATIONS

Our study suggests that the divergent shifts among co-occurring species along the same elevation gradients could be attributed to both multivariate environmental variations and species-specific plant responses. Multivariate environmental variations are characterized with elevation variations in soil water, soil nutrient, and growth space in our study. The species-specific responses arose from the functional dissimilarities. Therefore, integrating information on environmental variation and plant functional traits could inform predictions of species shifts (e.g., Zhai et al. (2016)). The trait-based predictions of species distribution have already been applied on a global scale. For example, van Bodegom and Douma (2014) derived global trait maps based on the association between traits and multiple environmental drivers. This study also characterized nine globally representative vegetation types based on their trait combinations. Importantly, valid distribution predictions of these vegetation types were made by the trait maps. The potential of trait-based prediction for local conservation is well supported by the findings from our study. Notably, prediction at a local scale can use plant traits to directly characterize species of interest, instead of the artificial vegetation types used on the global scale.

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LITERATURE CITED

- Ågren, G. I., J. Å. M. Wetterstedt, and M. F. K. Billberger. 2012. Nutrient limitation on terrestrial plant growth – modeling the interaction between nitrogen and phosphorus. *New Phytologist* 194:953–960.
- Asner, G. P., et al. 2017. Scale dependence of canopy trait distributions along a tropical forest elevation gradient. *New Phytologist* 214:973–988.
- Averill, C., and A. Finzi. 2011. Increasing plant use of organic nitrogen with elevation is reflected in nitrogen uptake rates and ecosystem $\delta^{15}\text{N}$. *Ecology* 92:883–891.
- Brookshire, E. N. J., P. C. Stoy, B. Currey, and B. Finney. 2020. The greening of the Northern Great Plains and its biogeochemical precursors. *Global Change Biology* 26:5404–5413.
- Buri, A., C. Cianfrani, E. Pinto-Figueroa, E. Yashiro, J. E. Spangenberg, T. Adatte, E. Verrecchia, A. Guisan, and J.-N. Pradervand. 2017. Soil factors improve predictions of plant species distribution in a mountain environment. *Progress in Physical Geography: Earth and Environment* 41:703–722.
- Cannone, N., and S. Pignatti. 2014. Ecological responses of plant species and communities to climate warming: upward shift or range filling processes? *Climatic Change* 123:201–214.
- Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261.
- Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10:1135–1142.
- Elser, J. J., W. F. Fagan, A. J. Kerckhoff, N. G. Swenson, and B. J. Enquist. 2010. Biological stoichiometry of plant production: Metabolism, scaling and ecological response to global change. *New Phytologist* 186:593–608.
- Fajardo, A., and F. I. Piper. 2017. An assessment of carbon and nutrient limitations in the formation of the southern Andes tree line. *Journal of Ecology* 105:517–527.
- Farquhar, G. D., and T. D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology* 33:317–345.
- Fei, S., J. M. Desprez, K. M. Potter, I. Jo, J. A. Knott, and C. M. Oswalt. 2017. Divergence of species responses to climate change. *Science Advances* 3:e1603055.
- Fisher, J. B., Y. Malhi, I. C. Torres, D. B. Metcalfe, M. J. van de Weg, P. Meir, J. E. Silva-Espejo, and W. H. Huasco. 2013. Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. *Oecologia* 172:889–902.
- Fry, B., A. L. Bern, M. S. Ross, and J. F. Meeder. 2000. $\delta^{15}\text{N}$ studies of nitrogen use by the red mangrove, *Rhizophora mangle* L. in south Florida. *Estuarine, Coastal and Shelf Science* 50:291–296.
- Gessler, A., M. Schaub, and N. G. McDowell. 2017. The role of nutrients in drought-induced tree mortality and recovery. *New Phytologist* 214:513–520.
- Griffin-Nolan, R. J., et al. 2018. Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes. *Functional Ecology* 32:1746–1756.
- Guo, F., J. Lenoir, and T. C. Bonebrake. 2018. Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications* 9:1315.
- Hagedorn, F., K. Gavazov, and J. M. Alexander. 2019. Above- and belowground linkages shape responses of mountain vegetation to climate change. *Science* 365:1119–1123.
- He, N., C. Liu, M. Tian, M. Li, H. Yang, G. Yu, D. Guo, M. D. Smith, Q. Yu, and J. Hou. 2018. Variation in leaf anatomical traits from tropical to cold-temperate forests and linkage to ecosystem functions. *Functional Ecology* 32:10–19.
- Hodgson, J. G., et al. 2011. Is leaf dry matter content a better predictor of soil fertility than specific leaf area? *Annals of Botany* 108:1337–1345.
- Inglett, P. W., K. R. Reddy, S. Newman, and B. Lorenzen. 2007. Increased soil stable nitrogen isotopic ratio following phosphorus enrichment: historical patterns and tests of two hypotheses in a phosphorus-limited wetland. *Oecologia* 153:99–109.
- Johnson, P. S., S. R. Shifley, and R. Rogers. 2009. The ecology and silviculture of oaks. CABI Publishing, New York, New York, USA and Oxford, UK.
- Kattge, J., et al. 2020. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* 26:119–188.
- Kling, M. M., S. L. Auer, P. J. Comer, D. D. Ackerly, and H. Hamilton. 2020. Multiple axes of ecological vulnerability to climate change. *Global Change Biology* 26:2798–2813.
- Körner, C. 2007. The use of ‘altitude’ in ecological research. *Trends in Ecology & Evolution* 22:569–574.
- Körner, C., G. D. Farquhar, and Z. Roksandic. 1988. A global survey of carbon isotope discrimination in plants from high altitude. *Oecologia* 74:623–632.
- Lajtha, K., and J. Getz. 1993. Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. *Oecologia* 94:95–101.
- LaRue, E. A., J. D. Holland, and N. C. Emery. 2018. Environmental predictors of dispersal traits across a species’ geographic range. *Ecology* 99:1857–1865.
- Legendre, P., and L. Legendre. 1998. Numerical ecology. Second edition. Elsevier, Amsterdam, Netherlands.
- Legendre, P., and J. Oksanen. 2018. lmodel2: model II regression. R package version 1.7-3. <https://cran.r-project.org/package=lmodel2>
- Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* 38:15–28.
- Li, C., C. Wu, B. Duan, H. Korpelainen, and O. Luukkanen. 2009. Age-related nutrient content and carbon isotope composition in the leaves and branches of *Quercus aquifolioides* along an altitudinal gradient. *Trees* 23:1109–1121.
- Lovett, G. M., and J. D. Kinsman. 1990. Atmospheric pollutant deposition to high-elevation ecosystems. *Atmospheric Environment*. Part A. General Topics 24:2767–2786.
- Matteodo, M., S. Wipf, V. Stöckli, C. Rixen, and P. Vittoz. 2013. Elevation gradient of successful plant traits for colonizing alpine summits under climate change. *Environmental Research Letters* 8:024043.
- Maxwell, T. M., L. C. R. Silva, and W. R. Horwath. 2018. Integrating effects of species composition and soil properties to predict shifts in montane forest carbon–water relations.

- Proceedings of the National Academy of Sciences of the United States of America 115:4219–4226.
- Mayor, J. R., et al. 2017. Elevation alters ecosystem properties across temperate treelines globally. *Nature* 542:91–95.
- McElwain, J. C. 2004. Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO₂ partial pressure. *Geology* 32:1017–1020.
- Miller, K. M., and B. J. McGill. 2018. Land use and life history limit migration capacity of eastern tree species. *Global Ecology and Biogeography* 27:57–67.
- Möhl, P., et al. 2019. Twelve years of low nutrient input stimulates growth of trees and dwarf shrubs in the treeline ecotone. *Journal of Ecology* 107:768–780.
- Normand, S., U. A. Treier, C. Randin, P. Vittoz, A. Guisan, and J.-C. Svenning. 2009. Importance of abiotic stress as a range-limit determinant for European plants: Insights from species responses to climatic gradients. *Global Ecology and Biogeography* 18:437–449.
- Oksanen, J. 2020. *vegan: community ecology package*. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Ouyang, S., et al. 2019. Effects of stand age, richness and density on productivity in subtropical forests in China. *Journal of Ecology* 107:2266–2277.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Pérez-Harguindeguy, N., et al. 2013. New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany* 61:167–234.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2019. *nlme: linear and nonlinear mixed effects models*. R package version 3.1-117. <https://cran.r-project.org/package=nlme>
- R Core Team. 2020. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rapacciuolo, G., et al. 2014. Beyond a warming fingerprint: Individualistic biogeographic responses to heterogeneous climate change in California. *Global Change Biology* 20:2841–2855.
- Rehm, E. M., and K. J. Feeley. 2015. The inability of tropical cloud forest species to invade grasslands above treeline during climate change: Potential explanations and consequences. *Ecography* 38:1167–1175.
- Rigling, A., et al. 2013. Driving factors of a vegetation shift from Scots pine to pubescent oak in dry Alpine forests. *Global Change Biology* 19:229–240.
- Robinson, D., L. Handley, C. Scrimgeour, D. Gordon, B. Forster, and R. Ellis. 2000. Using stable isotope natural abundances ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to integrate the stress responses of wild barley (*Hordeum spontaneum* C. Koch.) genotypes. *Journal of Experimental Botany* 51:41–50.
- Rosbakh, S., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and P. Poschod. 2017. Contrasting effects of extreme drought and snowmelt patterns on mountain plants along an elevation gradient. *Frontiers in Plant Science* 8:1478.
- Rumpf, S. B., K. Hülber, N. E. Zimmermann, and S. Dullinger. 2019. Elevational rear edges shifted at least as much as leading edges over the last century. *Global Ecology and Biogeography* 28:533–543.
- Schimel, J. P., and J. Bennett. 2004. Nitrogen mineralization: Challenges of a changing paradigm. *Ecology* 85:591–602.
- Seibt, U., A. Rajabi, H. Griffiths, and J. A. Berry. 2008. Carbon isotopes and water use efficiency: sense and sensitivity. *Oecologia* 155:441–454.
- Sigdel, S. R., Y. Wang, J. J. Camarero, H. Zhu, E. Liang, and J. Peñuelas. 2018. Moisture-mediated responsiveness of treeline shifts to global warming in the Himalayas. *Global Change Biology* 24:5549–5559.
- Sokal, R., and F. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. W. H. Freeman and Company, New York, New York, USA.
- Stahl, U., J. Kattge, B. Reu, W. Voigt, K. Ogle, J. Dickie, and C. Wirth. 2013. Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies. *Ecosphere* 4:art128.
- Stanton, M. L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65:1105–1112.
- Umaña, M. N., and N. G. Swenson. 2019. Intraspecific variation in traits and tree growth along an elevational gradient in a subtropical forest. *Oecologia* 191:153–164.
- van Bodegom, P. M., J. C. Douma, and L. M. Verheijen. 2014. A fully traits-based approach to modeling global vegetation distribution. *Proceedings of the National Academy of Sciences of the United States of America* 111:13733–13738.
- Van de Water, P. K., S. W. Leavitt, and J. L. Betancourt. 2002. Leaf $\delta^{13}\text{C}$ variability with elevation, slope aspect, and precipitation in the southwest United States. *Oecologia* 132:332–343.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Vitousek, P. M., C. B. Field, and P. A. Matson. 1990. Variation in foliar $\delta^{13}\text{C}$ in Hawaiian *Metrosideros* polymorpha: a case of internal resistance? *Oecologia* 84:362–370.
- Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications* 20:5–15.
- Wang, A., et al. 2018. Elevation alters carbon and nutrient concentrations and stoichiometry in *Quercus aquifolioides* in southwestern China. *Science of the Total Environment* 622–623:1463–1475.
- Wang, W. J., F. R. Thompson III, H. S. He, J. S. Fraser, W. D. Dijak, and T. Jones-Farrand. 2019. Climate change and tree harvest interact to affect future tree species distribution changes. *Journal of Ecology* 107:1901–1917.
- Wason, J. W., and M. Dovciak. 2017. Tree demography suggests multiple directions and drivers for species range shifts in mountains of Northeastern United States. *Global Change Biology* 23:3335–3347.
- Wu, M. S., S. J. Feakins, R. E. Martin, A. Shenkin, L. P. Bentley, B. Blonder, N. Salinas, G. P. Asner, and Y. Malhi. 2017. Altitude effect on leaf wax carbon isotopic composition in humid tropical forests. *Geochimica Et Cosmochimica Acta* 206:1–17.
- Wu, Z., and P. H. Raven. 1999. *Flora of China*. Science Press, Beijing, China and Missouri Botanical Garden, St. Louis, Missouri, USA.
- Zhai, L., J. Jiang, D. DeAngelis, and L. da Silveira Lobo Sternberg. 2016. Prediction of plant vulnerability to salinity increase in a coastal ecosystem by stable isotope composition ($\delta^{18}\text{O}$) of plant stem water: A model study. *Ecosystems* 19:32–49.
- Zhai, L., E. J. Jokela, S. A. Gezan, and J. G. Vogel. 2015. Family, environment and silviculture effects in pure- and mixed-family stands of loblolly (*Pinus taeda* L.) and slash (*P. elliottii* Engelm. var. *elliottii*) pine. *Forest Ecology and Management* 337:28–40.
- Zhai, L., K. W. Krauss, X. Liu, J. A. Duberstein, W. H. Conner, D. L. DeAngelis, and L. da Silveira Lobo Sternberg. 2018. Growth stress response to sea level rise in species with contrasting functional traits: A case study in tidal freshwater forested wetlands. *Environmental and Experimental Botany* 155:378–386.

- Zhang, X., B. Zhang, K. Feeley, G. G. Wang, J. Zhang, and L. Zhai. 2019. Ecological contingency in species shifts: Down-slope shifts of woody species under warming climate and land-use change. *Environmental Research Letters* 14: 114033.
- Zhao, N., G. Yu, N. He, F. Xia, Q. Wang, R. Wang, Z. Xu, and Y. Jia. 2016. Invariant allometric scaling of nitrogen and phosphorus in leaves, stems, and fine roots of woody plants along an altitudinal gradient. *Journal of Plant Research* 129:647–657.

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