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# Climate and multiple dimensions of plant diversity regulate ecosystem carbon exchange along an elevational gradient

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**Abstract.** The impacts of warming on communities and ecosystems are predicted to be significant in mountain ecosystems because physiological processes, including rates of carbon (C) cycling, are often more temperature-sensitive in colder environments. Plant biodiversity can also influence C exchange, yet few studies integrate how biotic and abiotic factors may directly or interactively impact ecosystem C flux. Here, we examine the link between simultaneous changes in multiple dimensions of plant diversity and peak growing season ecosystem C uptake across a climatic gradient in the Rocky Mountains, Colorado, USA. We found that taxonomic diversity (species richness), functional diversity (functional evenness), and phylogenetic diversity (mean pairwise distance) were significantly and positively related to peak growing season ecosystem C uptake (i.e., net ecosystem exchange) when considered independently. However, when abiotic and biotic factors were integrated in a structural equation model, only plant phylogenetic diversity was significantly related to C uptake. In addition, we found that actual evapotranspiration (AET—a measure that integrates precipitation and temperature) affected ecosystem C exchange indirectly via its impact on the three dimensions of plant diversity that we examined. These findings highlight complex relationships among key measures of biodiversity and ecosystem C uptake in a rapidly warming ecosystem, and the possible mechanisms that underlie relationships between biodiversity and ecosystem functioning. They also point to the need for integrating multiple dimensions of biodiversity into studies of community and ecosystem ecology.

**Key words:** abiotic; biodiversity; ecosystem carbon dynamics; elevational gradient; NEE; net ecosystem exchange; plant.

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## INTRODUCTION

For over 100 yr (see von Humboldt 1849, Grinnell 1924), elevational gradients have provided information on how temperature and associated environmental factors that change with elevation (Körner, 2007*a, b*) influence species, communities, and ecosystem functions (Kivlin et al. 2014, Read et al. 2014, Mayor et al. 2017). More recently, research has turned to investigating how plant diversity might directly regulate ecosystem function (Tilman et al. 1997, 2014). However, climate and species are not independent—the distribution, abundance, diversity, and phenologies of species (Pauli et al. 2001, Dunne et al. 2003, Gian-Reto 2010, Dorji et al. 2013) are all directly and/or indirectly impacted by abiotic factors. Thus, investigating and partitioning the relative biotic and abiotic controls on ecosystem function, particularly on carbon cycling and storage, is an active area of research, especially as biodiversity and climate are both shifting with global change.

Carbon (C) dynamics are critical to understand as they are climatically sensitive, govern the productivity of ecosystems, and directly or indirectly impact many other ecosystem functions (Heimann and Reichstein 2008, Chapin et al. 2009, McGuire et al. 2018). Recent work highlighted how, across ecosystem types, experimental warming increased aboveground biomass and soil respiration, with net primary productivity remaining largely unaltered (Song et al. 2019). Further, net ecosystem carbon fluxes did not respond to warming across ecosystems, likely due to large site-level variation in soil moisture and soil properties, net ecosystem CO<sub>2</sub> exchange (NEE), and gross primary productivity (Song et al. 2019). Harnessing information about environmental variation, the functional traits of organisms, evolutionary history, and taxonomic diversity may yield better predictions of the ecosystem-level consequences of shifting biodiversity along environmental gradients and is a promising approach in community and ecosystem ecology.

Mountain ecosystems are particularly sensitive to environmental change, and they are important for local and global C cycling, harboring significant soil C stocks (Sundqvist et al. 2013), making mountain ecosystems excellent places to test how climate and biodiversity impact ecosystem

function. The topography in mountain ecosystems creates heterogeneous climate environments as well as plant communities that have traits that respond to climatic heterogeneity. Taking advantage of the heterogeneity across elevational gradients to understand the responses of community and ecosystems to environmental changes over time and space has led to important ecological discoveries (Fukami and Wardle 2005, Walker et al. 2010, Mayor et al. 2017), and as global change experiments may underestimate some community- and ecosystem-scale responses to variation in climate (Wolkovich et al. 2012), utilizing observational gradients can be a fruitful path forward. Yet, few studies examine how variation in abiotic conditions (e.g., temperature and precipitation) directly and indirectly impact both biodiversity and ecosystem function, while simultaneously evaluating the influence of multiple dimensions of diversity (e.g., functional, phylogenetic, taxonomic) on ecosystem C dynamics, and studies that do explore multiple dimensions of biodiversity often come to different conclusions.

In this study, we examined the relationships among C dynamics, multiple dimensions of plant diversity, and climate at 12 sites located along an elevational gradient (2480–3560 m) in the Colorado Rockies. In particular, we tested two hypotheses: (1) environmental variables (i.e., precipitation, temperature), will be the most important driver of peak growing season ecosystem C uptake in this ecosystem as photosynthesis and plant and ecosystem respiration are highly sensitive to environmental conditions, and (2) environmental factors may indirectly impact ecosystem C uptake via their effects on plant diversity because plant community dynamics, such as competition and facilitation, are often governed by abiotic factors and scale up to affect ecosystem properties and functions. Therefore, integrating multiple dimensions of plant diversity and climatic variables into the same model will improve our understanding of the relative effects of abiotic and biotic factors on ecosystem C uptake.

## METHODS

### Site description

We conducted this study near the Rocky Mountain Biological Laboratory in the West

Elk range of the southern Rocky Mountains in Colorado, USA. A total of 12 study sites (a  $10 \times 10$  m sampling area at each location along the gradient) were surveyed ranging in elevation from 2480 to 3560 m a.s.l., spaced, on average, every 100 m. All sites are located in open mountain meadows without tree cover. Mean summertime temperature, derived from the Worldclim dataset and defined as an average over the warmest quarter, ranged across the elevational range from  $8.3^\circ$  to  $14.3^\circ\text{C}$ , and mean summertime precipitation, defined as the average precipitation over the warmest quarter, ranged from 355 to 679 mm/yr (Hijmans et al. 2005); temperature decreased, and precipitation increased with increasing elevation (Fig. 1). In a previous study, these long-term temperatures were shown to correlate with weather station data at a select few sites ( $R^2 = 0.62$ ) and likely represent the climatic conditions and filters that have acted on perennial plant species in this system (Read et al. 2017). In June and July of 2015 (date dependent on the elevation of the site sampled, with lower elevation sites starting in June), at the peak of the growing season at each site, we conducted visual estimations of plant percent cover of all plant species and measured the peak growing season potential C uptake, in five randomly selected  $1\text{-m}^2$  plots at each site. These five plots were spaced roughly 5 m apart and were previously established (see Read et al. 2017), totaling 60 plots across the gradient ( $N = 60$  for all statistical analyses). In our system, plant percent cover is correlated with aboveground biomass (Appendix S1: Fig. S1). Additional information about each site along the elevational gradient is included in Tables 1 and 2 of the Supplemental Material and in Read et al. (2017).

#### Actual evapotranspiration

In order to integrate climatic information, and to minimize the number of collinear variables in our statistical analyses, we estimated actual evapotranspiration (AET) using Worldclim derived mean annual precipitation (MAP) and mean annual temperature (MAT) for each of the 12 sites along the elevational gradient. Here, AET is estimated based on Turc's formula (Turc 1954, Kluge et al. 2006) shown as follows:

$$\text{AET} = P / [0.09 + (P/L)^2]^{1/2} \quad (1)$$

where  $P$  is MAP (mm/yr),  $L = 300 + 25T + 0.05T^3$ , and  $T$  used to define  $L$  is MAT ( $^\circ\text{C}$ ). This estimate of AET is commonly used in studies examining global trends in plant diversity (e.g., Spehn et al. 2012), and it is strongly related to ecosystem productivity at regional and local spatial scales (Yuan et al. 2010, Garbulsky et al. 2010, Zhang et al. 2017).

#### Ecosystem $\text{CO}_2$ exchange and canopy leaf area

During the peak of the growing season (mid-July 2015, depending on the elevation of the site), we used a Li-Cor 7500 infrared gas analyzer (IRGA; Li-Cor, Lincoln, Nebraska, USA) to measure changes in  $\text{CO}_2$  concentration, and a thermometer to measure air temperature, in each of the five plots at each of the 12 sites. We placed the IRGA inside a  $1\text{-m}^3$  cube that was made from a polyvinyl chloride (PVC) frame and transparent plastic sheeting, with internal fans to ensure adequate mixing of air and consistent chamber temperatures, sealed to the ground with two heavy chains. Each measurement cycle began by lowering the chamber, sealing it, and once a consistent rate of  $\text{CO}_2$  exchange was achieved, we began logging a two to three minute flux measurement in the light at a sampling frequency of 0.5 Hz. Once we completed a flux measurement, we opened the chamber, returning the plot to ambient  $\text{CO}_2$  concentrations ( $\sim 400$  ppm) before logging a second flux. We repeated this cycle three times, yielding three  $\text{CO}_2$  flux measurements per plot per site. For each study plot, we averaged the three fluxes made in the light and we calculated net ecosystem exchange (NEE;  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) as a measure of peak season potential C uptake, using Eq. 2 to quantify the continuous exchange of  $\text{CO}_2$  between the atmosphere, vegetation, and soil at peak growing season.

$$\text{NEE} = (\rho \times V \times (dC/dt)/A) \quad (2)$$

In Eq. 2,  $\rho$  is the air density ( $\text{mol air}/\text{m}^3$ ), defined as  $P/RT$ , where  $P$  is the average pressure (Pa),  $R$  is the ideal gas constant ( $8.314 \text{ J}\cdot\text{mol}^{-1}\cdot\text{air K}^{-1}$ ), and  $T$  (K) is the mean temperature.  $V$  is the chamber volume ( $\text{m}^3$ ),  $dC/dt$  is the slope of the chamber  $\text{CO}_2$  concentration against time ( $\mu\text{mol}\cdot\text{CO}_2 \text{ mol}^{-1}\cdot\text{air s}^{-1}$ ), and  $A$  is the surface

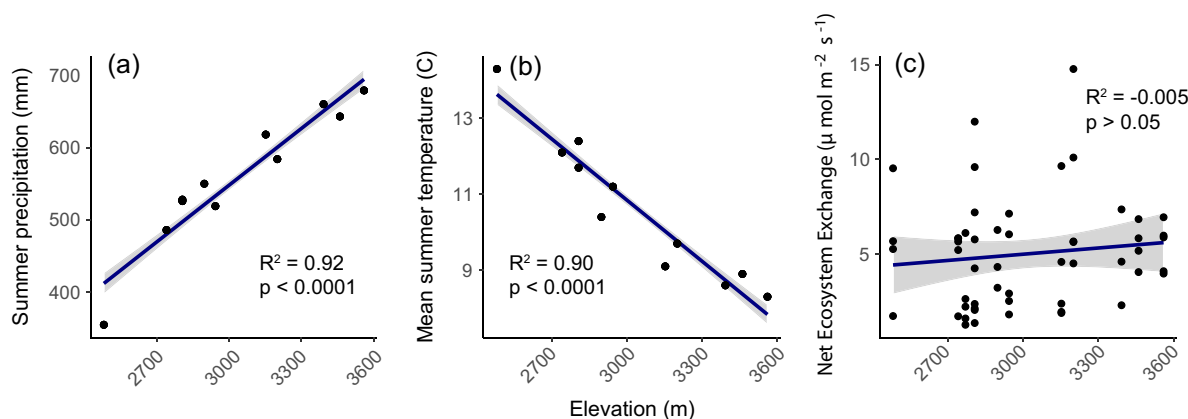


Fig. 1. Relationship of precipitation and temperature variation with elevation, using climatic data derived from the WorldClim database. With increasing elevation (a) precipitation increases, (b) temperature decreases, and (c) net ecosystem exchange (measured in this study) is unresponsive.

area of the ground ( $\text{m}^2$ ) within the chamber. We converted  $\text{CO}_2$  concentrations to dry mole fractions prior to calculating NEE. For consistency and clarity in our structural equation models, for all of our statistical analyses, we multiplied our raw NEE values by negative one; therefore, negative NEE values indicate fluxes from the ecosystem to the atmosphere and positive values indicate fluxes to the ecosystem from the atmosphere.

To calculate leaf area index (LAI;  $\text{m}^2$  leaf/ $\text{m}^2$  ground) in each plot, we obtained photosynthetically active radiation (PAR) measurements from above and below the canopy in each plot using a QSO-S PAR Photon Flux sensor (Decagon Devices, Pullman, Washington, USA). In addition, we recorded the time of each measurement and the latitude and longitude of each sampling location. We then used location, zenith angle, and beam fractionation (to estimate light attenuation through the canopy) to calculate LAI (see supplemental information) for each plot. LAI in this ecosystem is a reliable proxy for above-ground biomass and plant percent cover (Appendix S1: Fig. S1).

#### Trait data

In June and July of 2015 (date dependent on the elevation of each site, see Appendix S1: Table S1), we collected leaves and roots of at least three individuals from, at least, the five most common species within each site (see Appendix

S1: Table S2) in order to measure two plant functional traits that are thought to be broadly linked to carbon-related ecosystem processes (Diaz et al. 2004): leaf mass per area (LMA) and specific root length (SRL). Specifically, LMA is generally correlated with leaf percent N and photosynthetic rates, with lower LMA values associated with higher photosynthetic rates and C gain (Lambers et al. 2006, Pérez-Harguindeguy et al. 2016). Further, SRL is the most commonly sampled fine root characteristic; it is often indicative of relative growth and allocation strategies, and is sensitive to environmental change across ecosystems (Ostonen et al. 2007). For these two trait measurements, we followed standardized trait measurement protocols outlined in Pérez-Harguindeguy et al. (2016). For LMA, we collected at least three fully expanded leaves from each individual. For sampling roots for SRL, we collected two to four 2.5 cm diameter, 15 cm long soil cores from the base of each sampled plant, following protocols from published studies (e.g., Tjoelker et al. 2005, Orwin et al. 2014, Kraft et al. 2015). For both LMA and SRL, we used an Epson flatbed scanner to obtain leaf and root area. We then weighed the scanned material, dried it for 48 h at  $60^\circ\text{C}$ , and weighed it again. We measured the area of the scanned leaf images, and the total length of the scanned root images, with ImageJ software (v 1.45s; Schneider et al. 2012), using the IJRhizo macro (Pierret et al. 2013) to automatically trace all roots in each image. We calculated

LMA ( $\text{g/m}^2$ ) by dividing the dry mass by the scanned area, and we calculated specific root length (SRL;  $\text{m/g}$ ) for each individual plant by dividing the total root length by the dry root mass. Additional information on the leaf and root trait protocols and trait data collection for this study can be found in Read et al. 2017.

In addition, we downloaded published trait data from the TRY plant trait database (Kattge et al. 2009) to examine whether including more species included in a second set of functional diversity indices impacted our analyses and findings. For these indices, we used two leaf functional traits important for plant and ecosystem C cycling: leaf dry matter content (LDMC) and leaf nitrogen concentration (LNC). These two traits were available for the greatest number of taxa in our total species pool, representing roughly 75% of total plant cover across sites (Garnier et al. 2007, Pakeman and Quested 2007).

### *Dimensions of biodiversity*

Recent research points to the benefits of using functional diversity (FD)—the type, range, and relative abundance of organismal traits in ecological communities—rather than taxonomic diversity (TD) for improving our mechanistic understanding of how and why biodiversity loss impacts ecosystem functioning and the services derived from these functions (Díaz et al. 2007, De Bello et al. 2010, Lavorel et al. 2013). However, trait-based approaches also have limitations, because it is difficult to determine which traits will be most relevant for a given ecosystem function. Measuring the relevant traits for all species in a given community can also be logistically challenging. Therefore, dimensions of diversity beyond TD and FD, such as phylogenetic diversity (PD), may capture those traits that ultimately influence ecosystem function across a wider range of species in a community (e.g., Cadotte 2015). For example, mean pairwise phylogenetic distance (MPD)—a measure of PD—can explain significantly more variation in primary productivity than either species richness or functional group richness (Cadotte et al. 2008). As such, taking a multidimensional approach to biodiversity is a more comprehensive strategy for understanding the mechanisms underlying diversity's influence on ecosystem function (Carroll et al. 2011, Le Bagousse-Pinguet et al. 2019).

We examined three dimensions of biodiversity: (1) trait-based functional diversity (FD), (2) phylogenetic diversity (PD), and (3) taxonomic diversity (TD). Functional diversity (FD) was characterized using functional evenness ( $F_{\text{Eve}}$ ; Vileger et al. 2008), implemented in the R package FD (Laliberte and Legendre 2010). We calculated functional evenness ( $F_{\text{Eve}}$ ) using standardized values of our sampled functional traits (LMA and SRL) and then again for the two traits obtained from the TRY database (LDMC and LNC)— $F_{\text{Eve}}$  quantifies the regularity with which species are distributed throughout a multidimensional functional space. If the species in a community are clustered within functional space,  $F_{\text{Eve}}$  will be low. We estimated phylogenetic diversity (PD) using mean pairwise distance (MPD), calculated using the picante package in R (Kembel et al. 2010) with phylogenetic relationships and branch lengths obtained from a locally stored phylogeny in phylomatic (Zanne et al. 2014), processed using Phylomatic V3 (Webb et al. 2008) and the ape (Paradis et al. 2004) and phytools (Revell 2012) packages in R. Mean pairwise distance (MPD) is the mean sum of the phylogenetic branch lengths between all species pairs within a community. We measured TD using the number of species in a community, species richness (SR), and the Shannon diversity index ( $H'$ ).

There are a variety of metrics used to quantify and understand levels of varying dimensions of diversity in communities and to explore how biodiversity impacts ecosystem functioning. While many studies compare and contrast multiple biodiversity metrics simultaneously using statistical techniques, we identified three measures of biodiversity using an a priori approach that prioritized both richness and divergence in communities. In order to quantify and understand phylogenetic diversity, we selected mean pairwise (MPD) distance as it can be abundance-weighted, accurately captures divergence in alpha diversity, and can drive ecosystem productivity and promote ecosystem stability (Cadotte et al. 2008, 2012, Tucker et al. 2017). For functional diversity, we chose to examine functional evenness as it is mathematically similar to MPD, and can effectively capture the distribution and abundance of species within the niche space of communities (Mason et al. 2005, Vileger et al.

2008). Finally, we examined species richness because it is most commonly used to explore causal relationships between taxonomic diversity and ecosystem productivity and carbon exchange (Naeem et al. 2016). For taxonomic diversity, we also evaluated the Shannon diversity ( $H'$ ) index as it is abundance-weighted and measures evenness within communities. Here, both FD and PD are abundance-weighted whereas TD is not. In addition, we used the FD package by Laliberté and Legendre (2010) to calculate community-weighted means (CWM) for our two functional plant traits, LMA and SRL, as many biogeochemical processes are often, on a first order basis, correlated with CWMs of resource economics traits (Diaz et al. 2004, De Bello et al. 2010, Lavorel et al. 2013, Cadotte 2017).

### Statistical analyses

We ran a series of bivariate regressions to examine the relationship between multiple dimensions of diversity and NEE as well as between all dimensions of biodiversity, and for LAI and NEE across elevation. We then used piecewise structural equation modeling (SEM) to test our hypotheses laid out above—SEM is a set of statistical techniques that allows for relationships among one or more independent variables and one or more dependent variables using a combination of regression and factor analysis (Mitchell 1992, Grace et al. 2012). We examined alternative models designed to test explicit hypotheses about the relationships among multiple dimensions of biodiversity, canopy leaf area (estimated using leaf area index; LAI), net ecosystem exchange (NEE), and elevation (along with associated environmental variables, precipitation, and temperature). All pathways in the piecewise SEMs include site as a random effect, as plot can be considered to be the residual of the linear mixed effects models (which comprise piecewise SEMs), which is a random factor by default. The influence of multiple dimensions of biodiversity and abiotic factors on ecosystem function were implemented in the R package piecewiseSEM, and we chose a piecewise model structure as it allowed for the incorporation of random effects. To address hypotheses about the relative contributions of both biotic and abiotic factors to NEE, we tested two SEM structures, one in which elevation captures much of the

potential environmental variation across the gradient and one where both measured abiotic variables (i.e., precipitation and temperature as captured by AET) were modeled. In all SEMs, missing paths between the three measured dimensions of diversity were significant ( $P < 0.01$ )—as metrics of biodiversity are inherently related—impacting overall model fit.

Before running SEM analyses, we log-transformed all data to meet assumptions of normality for linear regression analyses, and we ran sets of SEMs with elevation as both a quadratic and linear term. For NEE, we multiplied all values by negative one prior to data transformation. Therefore in all analyses, positive NEE values are fluxes to the ecosystem from the atmosphere.

## RESULTS

### *Bivariate relationships between abiotic variables, biodiversity metrics, and net ecosystem exchange*

Across the elevational gradient, precipitation increased ( $R^2 = 0.92$ ,  $P < 0.0001$ ) and temperature decreased ( $R^2 = 0.90$ ,  $P < 0.0001$ ) with elevation (Fig. 1a, b), but there was no relationship between NEE and elevation ( $R^2 = 0.005$ ,  $P > 0.05$ ; Fig. 1c). In addition, species richness (TD) and mean pairwise distance (PD) increased with increasing elevation and elevation explained 22% and 36% of the variation in each dimension of diversity, respectively (for both,  $P < 0.05$ ; Appendix S1: Fig. S2). There was no relationship between functional evenness (FD) and elevation ( $R^2 = 0.04$ ,  $P > 0.05$ ; Appendix S1: Fig. S2).

All three dimensions of biodiversity were positively associated with NEE; however, the amount of variance explained varied among biodiversity metrics (Fig. 2a–c). Species richness (SR) accounted for 26% of the variance in net ecosystem exchange (NEE), the highest explained by a dimension of biodiversity (Fig. 2a). Our measure of phylogenetic diversity (mean pairwise distance), accounted for ~20% of the variance in NEE (Fig. 2c), and although functional evenness ( $F_{Eve}$ ) was positively related to NEE, the amount of variance explained by FD was 11% (Fig. 2b). In addition, there was no relationship between FD, as calculated using traits derived from the TRY database (LDMC and leaf %N), and NEE (Appendix S1: Fig. S3). We assessed the

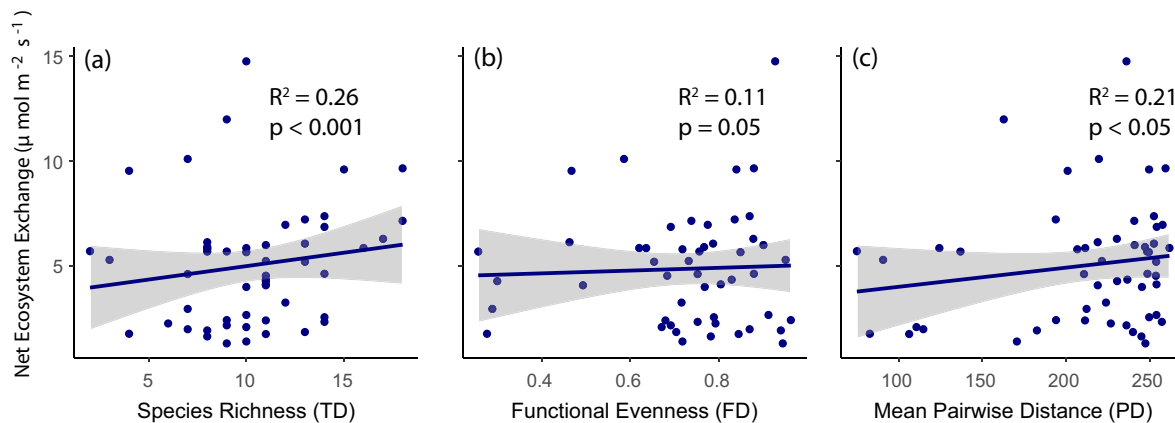


Fig. 2. Net ecosystem exchange (NEE) increases with increasing plant diversity. The strength of this relationship varies depending on the dimension of diversity considered, 95% confidence intervals shown as shaded area: (a) relationships between taxonomic diversity (SR) and NEE, (b) the relationship between functional diversity ( $F_{Eve}$ ) and peak growing season NEE, and (c) the relationship between phylogenetic diversity (MPD) and NEE.

relationships between biodiversity metrics, and we found that only species richness (TD) and mean pairwise distance (PD) were correlated with one another (see Appendix S1: Fig. S4).

There was no relationship between community-weighted means of either leaf mass per area (LMA) or specific root length (SRL) and NEE ( $P > 0.05$  for both traits), and there were no significant relationships of CWMs of LMA and SRL with elevation or with abiotic variables (results not presented).

#### Structural equation modeling

When we considered elevation as an abiotic factor that captures multiple axes of environmental variation along the gradient, the SEM explained 39% of the variance in NEE ( $n = 55$ ,  $C = 46.84$ ,  $df = 6$ ,  $P = 0.05$  Fig. 3a). We found that elevation had a significant, positive influence on all three dimensions of diversity (FD,  $z = 4.22$ ,  $P < 0.0001$ ; PD,  $z = 4.79$ ,  $P < 0.001$ ; TD,  $z = 4.02$ ,  $P < 0.0001$ ; Fig. 3a). However, elevation did not have a significant, direct effect on LAI or NEE, both when modeled as quadratic and linear. In addition, we found that phylogenetic diversity (PD) as measured by MPD and taxonomic diversity (TD) as measured by SR approached significance and were positively related to NEE ( $z = 2.03$ ,  $P < 0.05$ ;  $z = 3.91$ ,  $P < 0.0001$ ; Fig. 3a).

Next, we replaced elevation with its most important abiotic components, precipitation, and temperature and modeled them individually. We found that for precipitation, the model explained ~43% of the variance ( $n = 50$ ,  $C = 28.4$ ,  $df = 3$ ,  $P < 0.1$ ). Precipitation had a significant, positive influence on all three dimensions of diversity (FD,  $z = 6.64$ ,  $P < 0.0001$ ; PD,  $z = 5.72$ ,  $P < 0.001$ ; TD,  $z = 5.21$ ,  $P < 0.0001$ ), but precipitation did not directly affect LAI or NEE. In this model, both PD and TD were positively related to NEE ( $P < 0.02$  and  $0.33 \pm 0.15$ ,  $P < 0.05$ , respectively). When we used temperature as the sole abiotic variable, the model explained ~37% of the variance ( $n = 50$ ,  $C = 39.87$ ,  $df = 6$ ,  $P < 0.1$ ). In this model, temperature had a significant effect on all three dimensions of diversity (FD,  $z = -5.23$ ,  $P < 0.0001$ ; PD,  $z = -4.81$ ,  $P < 0.0001$ ; and, TD,  $z = -3.39$ ,  $P < 0.0001$ ), but was not significantly related to LAI or NEE. Finally, PD and TD were significantly related to NEE ( $z = 3.33$ ,  $P < 0.02$  and  $P < 0.01$ , respectively). Results for models that included the abundance-weighted Shannon diversity index were qualitatively the same as those that included species richness (results not shown).

We also combined variation in precipitation and temperature with elevation into one variable, that is, actual evapotranspiration (AET), and found that the model explained 47% of the

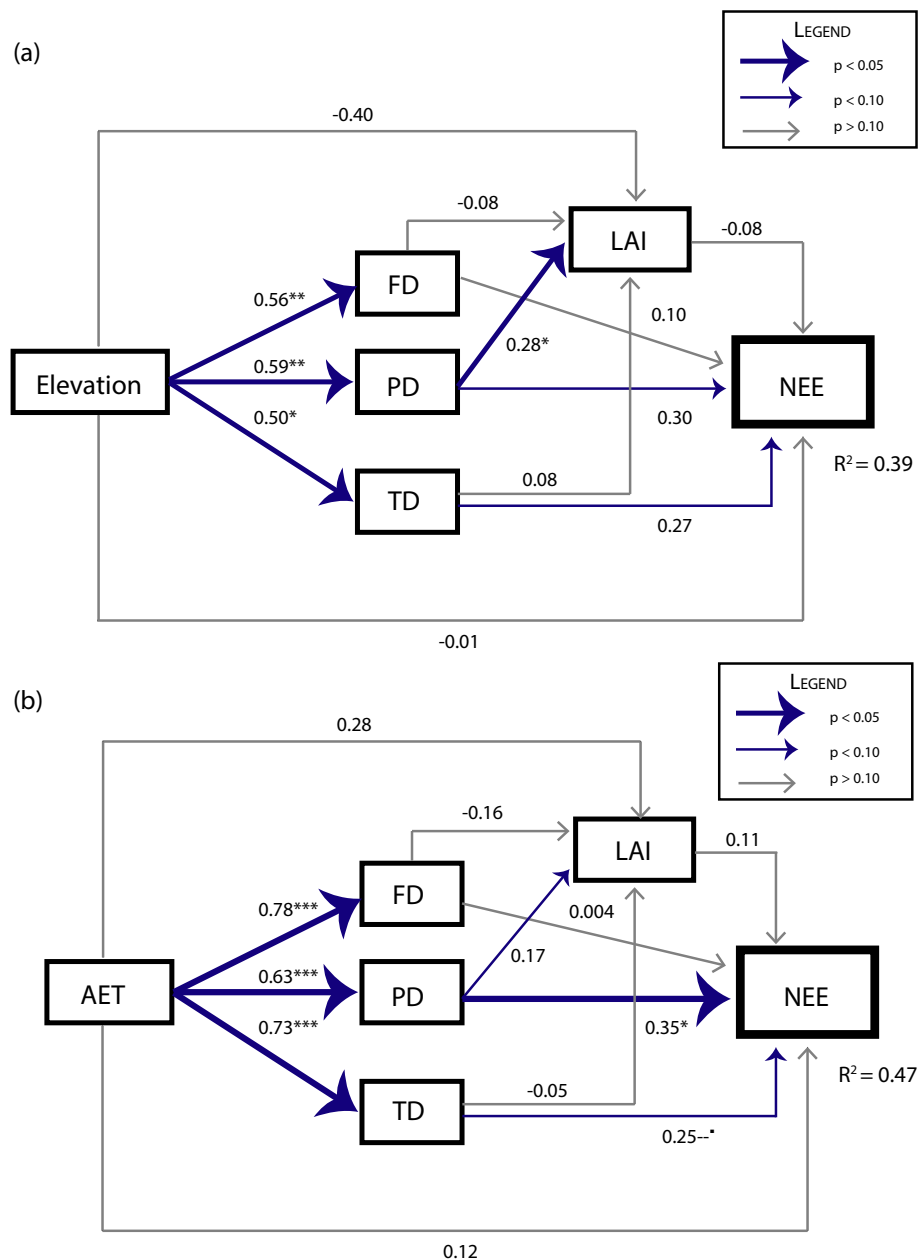


Fig. 3. Piecewise structural equation models (SEM) of the relative contributions of biotic (multidimensional biodiversity and canopy leaf area) and abiotic factors on peak growing season net ecosystem exchange (NEE). (a) The relationship between elevation, biotic factors, and NEE; and, (b) the relationship between actual evapotranspiration (AET), biotic factors, and NEE. Solid lines represent significant paths at  $P = 0.05$  and dashed lines represent non-significant paths; all significant path coefficients are indicated by an asterisk denoting level of significance (i.e., 0 = \*\*\*, 0.001 = \*\*, 0.01 = \*). Paths approaching significance are denoting by weighted dashed lines (i.e., paths where  $P < 0.1$ ). MAP, mean annual precipitation; FD, functional diversity (here, functional evenness); PD, phylogenetic diversity (here, mean pairwise distance); TD, taxonomic diversity (here, species richness); LAI, leaf area index; and, NEE, net ecosystem exchange.

variance in NEE ( $n = 50$ ,  $C = 25.62$ ,  $df = 6$ ,  $P = 0.05$ ; Fig. 3b). Here, AET was significantly and, positively, related to all three dimensions of diversity (FD,  $z = 6.76$ ,  $P < 0.0001$ ; PD,  $z = 4.91$ ,  $P < 0.0001$ ; and, TD,  $z = 7.51$ ,  $P < 0.0001$ ), but had no direct effect on LAI or NEE. In addition, PD was significantly, positively related to NEE and the positive relationship between TD and NEE approached significance ( $z = 3.10$ ,  $P < 0.001$ ;  $z = 1.72$ ,  $P < 0.1$ ; Fig. 3b). No other paths in the model were statistically significant. In addition, we repeated these analyses including CWMs for our two plant functional traits, LMA and SRL; however, the results were qualitatively the same, and with no significant paths between CWMs and LAI or NEE (results not presented). There was, however, a significant effect of AET on both LMA and RML (results not presented). In all SEMs, missing paths between the three measured dimensions of diversity were significant ( $P < 0.01$ ), impacting overall model fit.

## DISCUSSION

By using an elevational gradient, we examined the relationships among abiotic factors, peak growing season ecosystem C uptake, and multiple dimensions of plant diversity. Overall, we found that abiotic factors are strongly related to ecosystem C uptake, but these effects occur only indirectly through their relationships with multiple dimensions of plant diversity. In addition, across the gradient sampled in our study, these strong abiotic effects do not impact peak season ecosystem C uptake via their combined impact on canopy leaf area or aboveground biomass. Across the three dimensions of biodiversity measured, species richness explained the most amount of the variance (26%) in peak growing season net ecosystem exchange (NEE), followed by phylogenetic diversity (~20%) and functional evenness (11%) in bivariate analyses. Using structural equation models, we found that while elevation, precipitation, and temperature individually captured up to 43% of the variation in the SEM models, actual evapotranspiration (AET) was the best predictor (47%) of ecosystem C exchange, likely because it integrates precipitation and temperature. The finding that when considering all three dimensions of plant diversity simultaneously, using SEM models, PD

explains relatively more variance in NEE than other dimensions of plant diversity is novel, and it suggests that when exploring relationships between diversity and function across large environmental gradients, PD may be a better proxy for the diversity of plant traits thought to regulate a given function.

### *Abiotic factors impact peak growing season ecosystem C uptake indirectly*

We found strong relationships among temperature, precipitation, multiple dimensions of plant diversity, and net ecosystem carbon exchange (NEE) across the elevational gradient, and as predicted, precipitation and temperature significantly impacted peak growing season NEE. However, these abiotic effects were mediated by shifts in multiple dimensions of plant diversity (i.e., functional, phylogenetic, and taxonomic diversity). A large body of work has documented the importance of abiotic conditions for ecosystem C uptake and exchange across natural communities (Schimel et al. 2001, Huxman et al. 2003, Cleveland et al. 2011, Sloat et al. 2015), and a growing body of work has examined the contributions of both abiotic and biotic factors to ecosystem functioning in experimentally assembled communities (e.g., Zavaleta et al. 2003, Isbell et al. 2013). However, few have attempted to tease apart the relative contributions of abiotic and multiple biotic factors to ecosystem C uptake in natural ecosystems.

Because temperature often varies systematically with elevation in mountains, ecologists and biogeographers have long been aware of the value of elevational gradients for understanding how plant and animal communities respond to climate (e.g., von Humboldt 1849, Körner, 2007a, b, Sundqvist et al. 2013, Tito et al. 2020). Though we acknowledge that this is only one elevational gradient and our results may not extend to other systems, we highlight the strong effects that abiotic effects exert on ecosystem C uptake and exchange, but show that these occur only indirectly through their impacts on multiple dimensions of plant diversity. Notably, these strong abiotic effects do not impact peak growing season ecosystem C uptake simply through their combined impact on canopy leaf area or aboveground biomass. While this is in line with previous work in this system showing that net

ecosystem exchange is strongly regulated by temperature and precipitation (Sloat et al. 2015), our results highlight the importance of considering variation in multidimensional diversity in addition to the direct effects of abiotic factors.

#### *Multidimensional diversity and ecosystem C uptake*

Our study advances an understanding the nature of the relationship between biodiversity and ecosystem functioning in naturally assembled ecosystems that inherently capture variation in abiotic conditions (Grime 1998, Srivastava and Vellend 2005). For example, recent observational work across alpine grasslands found that the variation in aboveground production was better explained by functional composition (community-weighted mean trait values) than by taxonomic diversity (Jiang et al. 2016), pointing to the relationship between ecosystem properties and the identity of dominant species and their functional traits following the mass ratio hypothesis which suggests that the impact of the functional traits of species in ecosystems is dependent on the abundance of those species within a community (Grime 1998). Additionally, recent observational studies of broadleaved subtropical forest diversity found that decreased functional diversity and community-weighted mean traits, such as leaf mass per area, were linked to increasing aboveground biomass, supporting the mass ratio hypothesis, but that coarse woody production was influenced by both complementarity and mass ratio indirectly via their influence on canopy packing (Chiang et al. 2016). However, in our study, functional traits did not impact peak growing season ecosystem C uptake, suggesting that species richness and/or additional traits captured by phylogenetic diversity are more important in regulating C uptake along elevational gradients in mountains. Alternatively, our FD measure, limited by the generalized functional traits that we measured, may not have captured the traits that may be most closely linked to ecosystem C uptake and exchange across these ecosystems (e.g., nutrient status traits such as leaf nitrogen or physiological traits such as maximum photosynthetic rate, carbon use efficiency, or stomatal conductance).

While we observed significant plant diversity effects on peak growing season NEE, the magnitude of the effect depended on the dimension of

plant diversity examined. In particular, when we considered each dimension of diversity independently, we found positive, significant relationships with NEE but of varying strengths. However, when we considered all dimensions of plant diversity simultaneously using structural equation modeling (SEM), we found that only PD had a significant, positive effect on NEE. Thus, examining multiple dimensions of diversity simultaneously may facilitate inferences into the mechanisms underlying biodiversity's role in ecosystem functioning by highlighting different components of communities that may influence ecosystems (Naeem et al. 2016, Weeks et al. 2016). The finding that PD is most important for ecosystem C uptake runs contrary to recent work in temperate grasslands which found that taxonomic diversity (i.e., species richness) explained the variation in biomass production more than phylogenetic diversity, potentially because ecologically relevant trait variation was not explained by phylogenetic relatedness (Venail et al. 2015). It is possible that our study, spanning a substantial elevational gradient, captures a greater amount of phylogenetic diversity, especially given the partial turnover in taxonomic diversity between sites (see Appendix S1: Fig. S5), contributing to the greater influence of PD on peak growing season ecosystem C uptake our system vs. temperate grasslands. However, it is also possible that PD may be the most important dimension of plant diversity for peak growing season ecosystem C uptake in our study as it more broadly captures all phylogenetically conserved traits (e.g., maximum photosynthetic rate, foliar respiration in the dark, stomatal density) in a way in which FD falls short. This may be because FD was calculated for a limited number of traits sampled in this study—in principle it can include as many as we wish if using a multi-trait index. It is further in line with previous work that found PD to be the best predictor of ecosystem function, as phylogenetic relationships provide a more robust measure of the diversity among species that impacts ecosystem productivity than individual or small groups of traits (Cadotte et al. 2008).

#### *Conclusions*

By using an observational gradient in a mountain ecosystem, we were able to better understand and predict how the links between multiple

dimensions of plant diversity and peak growing season ecosystem C uptake are impacted by variation in abiotic conditions, and therefore rapid changes in environmental conditions attributable to climate change in this particular ecosystem. In addition, these findings highlight the complex relationships between key measures of plant diversity and ecosystem C uptake in a natural ecosystem—and the possible mechanisms that underlie relationships between biodiversity and ecosystem function—supporting the need for the integration of multiple dimensions of biodiversity into community and ecosystem ecology studies. In the coming decades, temperature and precipitation will continue to change, as will multiple dimensions of diversity in local communities. Experiments that manipulate multiple aspects of climate and multiple dimensions of biodiversity could enhance our ability to predict the responses of communities and the functions and services they provide. However, such experiments might prove unwieldy and overly expensive. Until such experiments are feasible, leveraging the power of elevational gradients as proxies for changes in climate is a fruitful path forward.

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