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RESEARCH ARTICLE

Plant functional traits are dynamic predictors of ecosystem functioning in variable environments

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Abstract

1. A central goal at the interface of ecology and conservation is understanding how the relationship between biodiversity and ecosystem function (B–EF) will shift with changing climate. Despite recent theoretical advances, studies which examine temporal variation in the functional traits and mechanisms (mass ratio effects and niche complementarity effects) that underpin the B–EF relationship are lacking.
2. Here, we use 13 years of data on plant species composition, plant traits, local-scale abiotic variables, above-ground net primary productivity (ANPP), and climate from the alpine tundra of Colorado (USA) to investigate temporal dynamics in the B–EF relationship. To assess how changing climatic conditions may alter the B–EF relationship, we built structural equation models (SEMs) for 11 traits across 13 years and evaluated the power of different trait SEMs to predict ANPP, as well as the relative contributions of mass ratio effects (community-weighted mean trait values; CWM), niche complementarity effects (functional dispersion; FDis) and local abiotic variables. Additionally, we coupled linear mixed effects models with Multimodel inference methods to assess how inclusion of trait–climate interactions might improve our ability to predict ANPP through time.
3. In every year, at least one SEM exhibited good fit, explaining between 19.6% and 57.2% of the variation in ANPP. However, the identity of the trait which best explained ANPP changed depending on winter precipitation, with leaf area, plant height and foliar nitrogen isotope content ($\delta^{15}N$) SEMs performing best in high, middle and low precipitation years, respectively. Regardless of trait identity, CWMs exerted a stronger influence on ANPP than FDis and total biotic effects were always greater than total abiotic effects. Multimodel inference reinforced the results of SEM analysis, with the inclusion of climate–trait interactions marginally improving our ability to predict ANPP through time.
4. *Synthesis*. Our results suggest that temporal variation in climatic conditions influences which traits, mechanisms and abiotic variables were most responsible for driving the B–EF relationship. Importantly, our findings suggest that future research should consider temporal variability in the B–EF relationship, particularly

how the predictive power of individual functional traits and abiotic variables may fluctuate as conditions shift due to climate change.

KEYWORDS
climate change, growing degree days, height, leaf area, mass ratio effects, niche complementarity, Niwot Ridge, winter precipitation

1 | INTRODUCTION

Global change has drastically altered ecosystem functioning by shifting patterns of biodiversity through species extinctions, range shifts and changes in abundance (Cardinale et al., 2012; De Laender et al., 2016). While early research on the biodiversity–ecosystem function (B–EF) relationship examined how changing levels of species richness might impact ecosystem function (Hooper et al., 2005; Tilman et al., 2001), recent advances show that functional trait distributions more strongly predict many ecosystem functions than species richness alone (Cadotte, 2017; Cadotte et al., 2011; de Bello et al., 2010; Gagic et al., 2015). Despite this theoretical advance in our understanding of the B–EF relationship, a recent large-scale experiment in European grasslands revealed that joint consideration of 41 functional traits was still only able to explain 12.7% of the variation in 42 ecosystem properties over a 10-year period (van der Plas et al., 2020). However, the same study showed that within individual years, functional traits were able to explain up to 32.6% of the variation in those ecosystem functions. While this discrepancy may be partially attributed to statistical issues with analysis (Hagan et al., 2023), the stark contrast in explanatory power between within-year and across-year models also suggests a biological explanation, specifically, that the strength of the B–EF relationship varies dynamically through time. Critically, we lack an understanding of what drives temporal variation in the B–EF relationship as most studies assume that the traits and/or mechanisms underlying the B–EF relationship are static (but see Armitage, 2016, 2017; Cardinale et al., 2007; Mori et al., 2017; Qiu & Cardinale, 2020) or fail to consider how the multiple functional mechanisms underlying the B–EF relationship operate simultaneously (Chiang et al., 2016; Mokany et al., 2008).

One source of temporal variation in the B–EF relationship may be a shift in which traits best predict ecosystem functions, leading certain traits to be more important during some years and unimportant in others depending on environmental conditions. While environmental context dependence in the B–EF relationship has been demonstrated in numerous systems including benthic macro-invertebrates (Geert Hiddink et al., 2009), mycorrhizal fungi (Jonsson et al., 2001) and temperate forests (Ratcliffe et al., 2017), these studies have generally quantified biodiversity in terms of taxonomic richness and have examined context dependence across spatial, not temporal, variation in environmental conditions. In one of the few studies to explore temporal dynamics in the ability of traits to predict ecosystem functions, Bongers et al. (2021) found that, in an experimental forest system, functional diversity metrics for multiple traits became more reliable predictors of accumulated stand volume as stand age increased. This temporal shift in the relationship between functional diversity and ecosystem function suggests that the predictive power of individual functional traits could trade-off in concert with changing environmental conditions. For example, a single trait may on average only explain a modest amount of variation in ecosystem function over long time periods because that trait is only predictive in 'good' years (high resource availability) while not being predictive in 'bad' years (low-resource availability) when a different trait associated with environmental stress serves as the best predictor. Considering how temporal fluctuations in environmental conditions modify the importance of specific traits could help resolve the seemingly low predictive power of functional traits for ecosystem functions through time.

A second source of temporal variation may arise from shifts in the functional mechanisms underlying the B–EF relationship. Two nonmutually exclusive mechanisms are typically invoked to explain the B–EF relationship: (1) niche complementarity and (2) mass ratio effects. Niche complementarity effects posit that ecosystem functioning should be maximized when species in a community use resources in complementary ways, leading to more complete and efficient consumption of the total resource pool. Because functional traits mediate how species interact with each other and their environment, communities containing a greater diversity of functional traits (often quantified as functional dispersion [FDis]; see Cadotte, 2017 and methods below) should be better able to engage in complementary resource use, thus enhancing their level of functioning (Petchey & Gaston, 2006; Tilman et al., 2001). In contrast, mass ratio effects focus on how the presence of high performing, dominant species control ecosystem function. Dominant species possess specific traits which confer high fitness and determine their large contributions to functioning; however, these traits should contribute to functioning regardless of individual species identity. Thus, community average trait values (often quantified as community weighted means [CWM]; see Cadotte, 2017 and methods below) can be used to capture relative differences in ecosystem functions (Grime, 1998).

While a large body of research has focussed on determining whether niche complementarity or mass ratio effects play a greater overall role in shaping ecosystem functions (Cardinale et al., 2007; Loreau & Hector, 2001; Wang et al., 2021), these mechanisms are not mutually exclusive (Chiang et al., 2016;

Mokany et al., 2008) and their relative importance can shift with changing environment conditions (Armitage, 2017). Studies have shown that, in natural systems, mass ratio effects are generally better predictors of individual ecosystem functions than niche complementarity effects (Fotis et al., 2018; Mokany et al., 2008; Needham et al., 2022; Tobner et al., 2016; van der Plas, 2019); however, research focussed on the stress gradient hypothesis suggests that the relative importance of these mechanisms may trade off as species interactions shift along stress/resource gradients (Baert et al., 2018; Bertness & Callaway, 1994; Fugère et al., 2012; Wang et al., 2013). For example, Wang et al. (2013) found that in an experimental grassland system, mass ratio effects tended to better explain net primary production in high-resource/low-stress environments where competition is thought to be the dominant interaction among species (Bertness & Callaway, 1994), while niche complementarity effects became more important in low-resource/high-stress environments where resource partitioning and facilitation are thought to be more prevalent (Bertness & Callaway, 1994; Wang et al., 2013; Wright et al., 2017). Most studies demonstrating this trade-off between B–EF mechanisms have evaluated changes along spatial environmental gradients; however, similar results should be expected within a site as environmental conditions change temporally, with mass ratio effects generally acting as better predictors of ecosystem function, but niche complementarity effects becoming more important during periods of high environmental stress.

Finally, while B–EF research often emphasizes the centrality of biotic mechanisms in shaping ecosystem functions, temporal variation in ecosystem functions can also be directly controlled by fluctuating abiotic conditions. For example, studies have found that in tundra ecosystems, temperature directly influences rates of plant litter decomposition, with higher temperatures leading to faster rates of decomposition independent of litter composition (Aerts, 2006; Hobbie, 1996). Similarly, short-term drought in tropical forest systems has been shown to shift biomass allocation patterns in tree communities from investment in above-ground to below-ground tissues without inducing shifts in species or functional diversity patterns (Doughty et al., 2014). Ultimately, abiotic conditions determine both the productive capacity and the biotic composition of ecosystems, and thus their direct and indirect influence (i.e. via changes in composition) should be considered concurrently in any complete assessment of the B–EF relationship (Brun et al., 2019).

Here, we couple long-term observational data from a natural system with structural equation models (SEMs) and linear mixed effects models to disentangle the complex temporal links between site-level climatic changes, local abiotic conditions, biodiversity patterns and ecosystem function (Grace, 2008; Pugesek et al., 2003). To explore these dynamics, we used 13 years of data (2008, 2010–2021) on local abiotic conditions, plant species composition, plant functional traits and above-ground net primary productivity (ANPP) collected in the alpine tundra of Colorado, USA, at the Niwot Ridge Long Term Ecological Research (LTER) site. During the last four decades, Niwot Ridge has experienced increasing winter precipitation (e.g. precipitation falling between October and May) and increasing summer temperatures (Bjarke et al., 2021; Kittel et al., 2015; McGuire et al., 2012). Climatic changes at Niwot Ridge (and in the Southern Rocky Mountain region generally) are correlated with shifts in the taxonomic and functional composition of alpine plant communities (Niwot Ridge LTER, unpublished data; Huxley & Spasojevic, 2021), making this an ideal system to disentangle the complex temporal nature of the B–EF relationship. We predict that: (1) functional traits associated with plant size (e.g. plant height and leaf area) should generally best predict ANPP, but the identity of the trait which best predicts ANPP will change during climatically stressful years with unusually high winter precipitation or summer temperatures; (2) mass ratio effects (measured as CWM traits values) will be the primary driver of ANPP, but during climatically stressful years niche complementarity effects (measured as FDis trait values) will become relatively more important than mass ratio effects; (3) biotic mechanisms (inferred from trait patterns) will generally play a stronger role in shaping ANPP than local abiotic conditions, but the influence of abiotic conditions will become more important during climatically stressful years; and (4) considering interactions between annual climatic conditions climate and biotic/abiotic variables will improve our ability to predict ANPP through time.

2 | METHODS

2.1 | Study site

This study uses data collected from alpine tundra on Niwot Ridge (40.03' N, 105.35' W) in the Front Range of the Rocky Mountains, approximately 40 km West of Boulder, CO, USA, a research site, which is managed by the Niwot Ridge Long Term Ecological Research Program (NWT). All data used in this study were collected and curated by NWT staff or researchers affiliated with NWT and are available for public use via the NWT Electronic Data Initiative portal (see 'Data Availability Statement' section and associated data package citations). Niwot Ridge has a very short growing season (8–10 weeks, June–August) and a long winter, leading to an average annual temperature of −2.2°C and an average annual precipitation of 930 mm that predominantly falls as snow (~75%; Bueno de Mesquita et al., 2021; Kittel et al., 2015; Knowles et al., 2015; McGuire et al., 2012; Williams et al., 2011). Annual wind speeds on Niwot Ridge average 8.1 m s^{-1} and winds typically blow from west to east (Litaor et al., 2008). Due to the stark topography and high wind speeds on Niwot Ridge, snow redistribution via wind is an important process for determining where snow accumulates on the landscape (Bowman & Seastedt, 2001; Greenland et al., 1984; Williams et al., 2009). Predictable patterns of snow accumulation generate high plant beta-diversity, with near-complete species turnover and differences of up to two orders of magnitude in productivity across gradients as short as 10 m (Spasojevic & Suding, 2012).

2.2 | Saddle climate data

NWT has maintained continuous, site-level measurements of temperature, precipitation and other climate variables in the 'Saddle' area of Niwot Ridge since 1982 (Bjarke et al., 2021). For the period of our study (2007–2021), daily mean and instantaneous minimum and maximum temperatures were recorded using a Campbell Instruments CR23X data logger (2007–2014) and a CR1000 data logger (2014–2021; Morse et al., 2022a). Temperature data quality assurance was performed by previous NWT climatologists up through 2014 and has been automated using the GCE Data Toolbox since September 2014. Daily precipitation was measured using Belfort weighing-bucket gauge with Alter shield and recorded by mechanical chart (Morse et al., 2022b). The bucket contains antifreeze to melt snow and prevent collected precipitation from freezing. For the period of our study (September 2007–August 2021), about 3.7% of raw temperature data and 13.7% of raw precipitation data were missing.

Prior to infilling missing data, we performed additional data quality control of temperature and precipitation data as recommended by Brunet et al. (2006) and Kittel (2009) to screen gross errors, tolerance tests, temporal coherence and spatial coherence. We used 24 stations at NWT LTER or in the region for spatial coherence checks and infilling. Geographic range of stations from Saddle are approximately 28 km south to 35 km north, 22 km east to 18 km west and 1248 m below to 206 m above. Because of documented blowing snow issues for precipitation at Saddle (Williams et al., 1998), precipitation events were reviewed when (1) Saddle was the only station in the region to record precipitation, (2) the only station of six at NWT to record precipitation and only 1–3 stations in the region recorded precipitation and (3) Saddle was the only station at NWT to not record precipitation. Additional QC removed 0.3% of temperature values and 1.1% of precipitation values for infilling.

We then followed regression infilling methods for NWT long-term records established by Kittel et al. (2015). Stations were prioritized in infilling based on geographic and elevational proximity to Saddle. We applied an overcatch correction factor of daily precipitation × 0.39 recommended by Williams et al. (1998) for October–May and four large snow events in the shoulder seasons (e.g. June, September). The most frequent source stations for infilling Saddle daily values were the NWT LTER D1 alpine station for precipitation (informed 36.4% of infill values) and replicate [HMP] instruments at Saddle (77.8%) for temperature.

After QC and gap-filling, daily temperature data were homogenized to account for instrument changes over the electronic record by adjusting temperature data to the most recent instrument at Saddle. We used a 1-year overlap period between the outgoing and incumbent Saddle temperature electronic instruments, as well as an independent, quality-controlled, gap-filled record spanning the entire period of instrument changes (AmeriFlux US-NR1) to apply conservative mean difference adjustments ranging from −0.96 to −1.5°C. We performed additional inhomogeneity tests for Saddle temperature and precipitation using R packages RHtestsV4 and RHtests_dlyPrcp (Wang, 2008a, 2008b; Wang & Feng, 2013), and Climatol (Guijarro, 2022). No breaks were detected for the study period that warranted further homogenization based on the station history (for full Saddle temperature and precipitation datasets see: White et al., 2023a, 2023b).

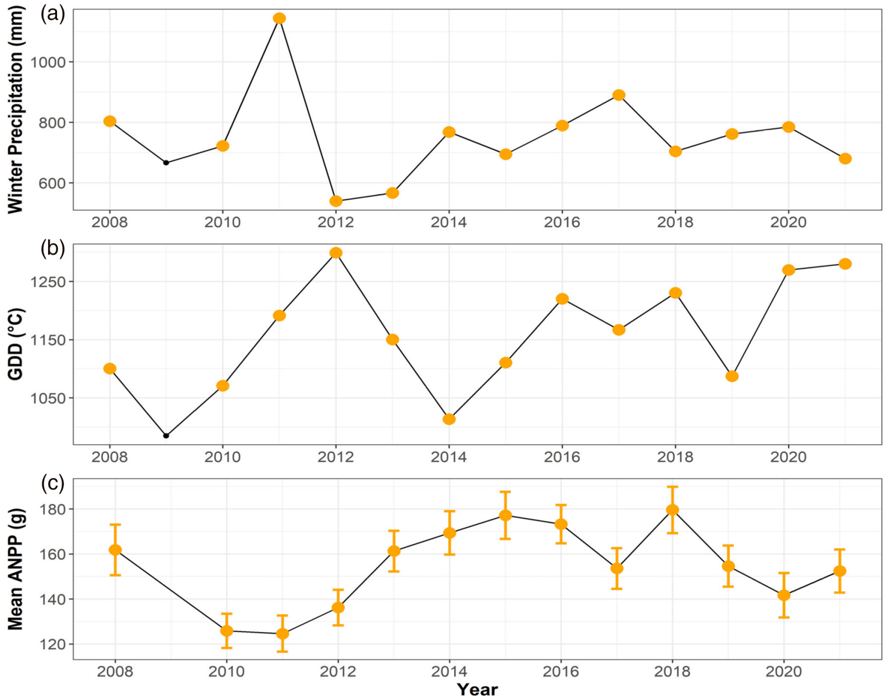
Two primary long-term trends have been detected in Niwot Ridge's climate record: (1) an increase in annual winter precipitation (Figure 1a) and (2) an increase in the annual number of growing degree days (Figure 1b; Bjarke et al., 2021; Kittel et al., 2015; McGuire et al., 2012). We calculated winter precipitation as the sum of all daily precipitation measurements recorded between October and May of the following calendar year. Annual growing degree days, on the contrary, were calculated as the sum of mean temperatures for all days where the mean temperature was greater than 0°C for each 'ecological year' (the period starting September 1 and finishing August 31 of the following year, hereafter referred to simply as year), as this time frame is more biologically relevant than the calendar year for alpine plant communities which experience their growing season between June and August.

2.3 | Saddle plot data

NWT has conducted long-term monitoring of alpine vegetation using 88 1 m^2 plots located in the Saddle. For each of these plots, comprehensive data exist on abiotic variables (topographic variables, snow-depth), biodiversity (species composition, functional traits) and ecosystem function (ANPP) over a 13-year period: 2008 and 2010–2021. Topography was quantified for each plot using three measures: elevation, aspect and slope. Elevation was estimated using a Trimble GPS with accuracy of ±3 m. Aspect was measured as the direction of a plot's downhill slope using a compass with a SIN transformation applied for analysis. Slope was quantified using the slope tool in ArcGIS 10.1. Snow-depth data were collected during irregularly timed snow surveys throughout fall, winter and spring months (September–June) by NWT technicians using snow poles, which estimate depth at 10 cm intervals (Walker, Morse, & Niwot Ridge LTER, 2022). Due to the irregular timing of snow-depth measurements throughout the year, we used mean snow-depth values for the month of May in our analysis as this month consistently contained at least one snow-depth survey (ranging between 1 and 3) and because May is typically when Niwot Ridge reaches peak snowpack (Litaor et al., 2008). Only 1 year (2008) lacked May snow-depth data, and for this year we used snow-depth data collected on April 29, 2008.

Plant species composition data for each Saddle plot were collected using point intercept methods (Walker, Humphries, et al., 2022). NWT staff mounted a 1 m^2 quadrat containing a 10 cm × 10 cm string grid on permanent plot corners and then vertically placed a pin flag at each of the 100 grid points, recording the identity of all species contacting the pin flag and their relative vertical position within the canopy. For our analyses, we only used

FIGURE 1 Climatic variables and above-ground net primary productivity measured in the Saddle region of Niwot Ridge from 2008 to 2021. Orange points indicate years included in our study (2008, 2010–2021). (a) Annual winter precipitation (between October and May) measured in centimeters; (b) Annual growing degree days (GDD; between September and August), measured as the sum of daily temperatures for days where mean daily temperature is greater than zero; (c) mean above-ground net primary productivity (ANPP) measured in grams across all 78 plots; error bars display standard error of ANPP.



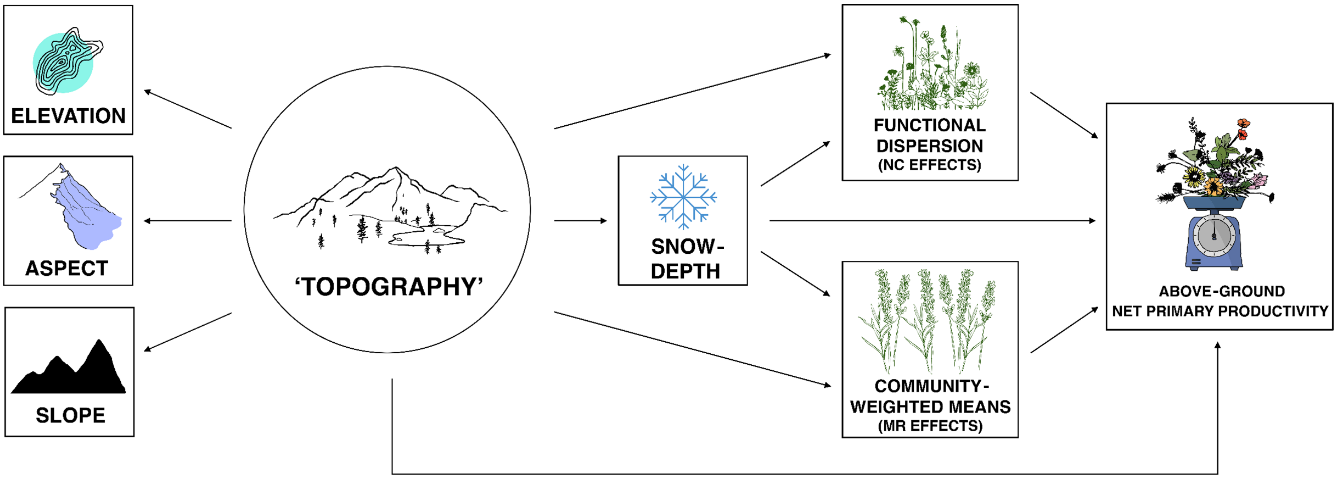


FIGURE 2 Structural equation model (SEM) meta-model used as the basis for SEMs across all traits and years. All pathways are based on research demonstrating causal pathways between topography, snow deposition, functional composition and above-ground net primary productivity in the alpine zone. 'Topography' is a latent variable constructed from elevation, aspect (sine transformed) and slope. Snow-depth is measured as average snow-depth for the month of May. All SEMs also included a snow-depth^2 term (omitted here for visual clarity) to account for the quadratic relationship between snow-depth and above-ground net primary productivity. Snow-depth^2 occupies the same model position as snow-depth; a covariation pathway was included between the two terms. Community-weighted mean trait values were used as a proxy for mass ratio effects (MR effects), while functional dispersion values were used as a proxy for niche complementarity effects (NC effects). A covariation term was included between the community weighted means and functional dispersion parameters. Above-ground net primary productivity was measured as the total annual above-ground vascular biomass harvested in 0.2 m × 0.5 m quadrats adjacent to each Saddle plot.

species composition data from the top-most 'hit' to calculate the relative abundance of each species in a plot to remain consistent with previous analyses of NWT's Saddle plot species composition (Spasojevic et al., 2013).

Above-ground net primary productivity (ANPP) data were collected by harvesting all nonwoody vascular biomass within 0.2 m × 0.5 m quadrats located near each Saddle plot (Figure 2c). Harvest locations were selected to replicate species composition and biomass distributions in each plot and were rotated annually to prevent overharvesting from any one area (Walker, Smith, et al., 2022). From 2008 to 2018, two biomass quadrats were harvested per Saddle plot; the mean of these harvests was calculated to produce a single measurement per plot. From 2019 to 2021, a single biomass quadrat was harvested per plot.

2.4 | Functional traits

NWT maintains a functional trait database (Spasojevic et al., 2022) that has trait data for 84.4% of species that have been found in the Saddle plots and identified to species level, with 55% of those species possessing habitat specific trait measurements (e.g. functional traits for *Geum rossii* measured independently in moist meadow, dry meadow and fell field habitats). In total, we have coverage of at least one trait for 98.3% of the total cover across the 13 years of our study. Eleven traits were included in this study: height, specific leaf area (SLA), leaf area, chlorophyll content, leaf dry matter content (LDMC), foliar per cent carbon content, foliar percent nitrogen content, foliar carbon to nitrogen ratio, foliar carbon isotope values ($\delta^{13}C$), foliar nitrogen isotope values ($\delta^{15}N$) and stomatal conductance. Height is indicative of a species' competitive ability for light (Westoby, 1998). SLA, LDMC, chlorophyll content and leaf chemistry traits are related to the leaf economics spectrum, which characterizes a species' capacity for stress tolerance versus resource acquisition (Osnas et al., 2013; Wright et al., 2004). Leaf area and stomatal conductance are related to a species' water/energy balance (Ackerly et al., 2002; Pérez-Harguindeguy et al., 2016). Finally, $\delta^{15}N$ is related to nitrogen uptake rates and N source (Craine et al., 2015). Trait measurements for each species or species × habitat combination were collected from at least 10 individuals in accordance with the protocols outlined in Pérez-Harguindeguy et al. (2016).

Using the trait values from the NWT functional trait database and the species composition data described in the previous section, we then used the 'dbfd' function from the 'FD' package in R version 4.1.1 to calculate single trait FDis, and community-weighted mean (CWM) trait values for each Saddle plot in every year (Laliberté & Legendre, 2010; Laliberté et al., 2014; R Core Team, 2021). Critically, we calculated CWM and FDis values using trait data weighted by species abundances not biomass to reduce circularity in the prediction of ANPP. In alpine systems, species abundance and biomass are not likely to be tightly correlated since many highly abundant species are quite small. Ten plots were discarded from these calculations in each year because they had either greater than 50% shrub or rock cover or were subject to long-term experimental snow-depth manipulation. Additional plots were discarded if we did not possess trait data for at least 80% of the vascular plant cover (plot number varied by specific trait and year; the number of plots retained for each SEM can be found in Appendix S1).

2.5 | Structural equation modelling

To explore links between the abiotic environment, biotic functional composition and ecosystem function, we built SEMs for each trait × year combination (e.g. leaf area SEMs for 2008, 2010, 2011, etc.). SEMs are useful for modeling complex ecological phenomena because they allow for the evaluation of both direct and indirect causal relationships among variables by estimating a global variance–covariance matrix (Bollen, 1989; Grace, 2006, 2008). All SEMs in this study used the same meta-model design (Figure 2), based on a robust body of research on alpine ecosystem dynamics at Niwot Ridge (Bowman & Seastedt, 2001; Bueno de Mesquita et al., 2018; Suding et al., 2015; Walker et al., 1993, 1994; Williams et al., 2015).

First, a latent variable representing 'topography' was constructed using direct measurements of elevation, aspect, and slope. Our inclusion of 'topography' as a latent variable was meant to capture uncertainty around this concept, as all aspects of topography (i.e. microtopographic variation) could not be directly measured. Topography is a major factor determining where snow deposition occurs on the alpine landscape, so we included a direct path from topography to snow-depth. Additionally, topography may influence biodiversity patterns and ANPP directly via factors independent of snow deposition (e.g. exposure to wind and solar radiation), so we included direct paths from topography to CWM and FDis trait values as well as ANPP. Next, we connected snow-depth directly to both trait metrics and ANPP, as snow deposition has been shown to influence levels of soil moisture, nutrient availability and growing season length, which fundamentally control biodiversity and productivity patterns (Bowman et al., 2003; Bowman & Seastedt, 2001; Litaor et al., 2008; Seastedt et al., 2004; Walker et al., 2001). We also added a snow-depth^2 term, with an identical model position to snow-depth, to account for snow-depth's quadratic relationship with ANPP where both low and high snow-depths can produce low levels of ANPP due to moisture limitation and energy limitation, respectively (Walker et al., 1993, 2001).

We then linked our functional trait indices (CWM and FDis) for each individual trait to ANPP, based on fundamental B–EF theory showing that ecosystem functions are simultaneously shaped by the average and variation of community trait values (Cadotte, 2017; Chiang et al., 2016). While some studies have shown that species niche differences are best summarized by multitrait models and/or metrics (Huang et al., 2020; Kraft et al., 2015), we chose to build separate SEMs for each trait (i.e. each SEM contains the CWM and FDis values for only one trait), for both biological and statistical reasons. Biologically, individual traits have been shown to strongly respond to environmental gradients in the alpine tundra of Niwot Ridge, while multitrait metrics (e.g. FDis calculated with multiple traits) often show no pattern due to opposing responses in individual traits (Spasojevic & Suding, 2012). Furthermore, building SEMs containing metrics for multiple individual traits is statistically challenging as the inclusion of multiple additional parameters would greatly exceed rule-of-thumb estimates for acceptable sample size when using SEMs (10 data points per observed variable; Bentler & Chou, 1987; Nunnally, 1967).

Finally, we included two covariation terms—one between snow-depth and snow-depth^2 and another between CWM and FDis. These covariation terms account for the fact that that these variable pairs are driven by the same causal links within the SEM and are likely to be correlated (highly correlated in the case of snow-depth and snow-depth^2) but are not causally related to one another. Using this meta-model structure, we built SEMs that incorporated the CWM and FDis values of each individual trait for each year. With 11 traits and 13 years of data, we could generate a total of 143 possible SEMs across all traits and years. All SEMs were constructed using the 'lavaan' package in R version 4.0.2 (Rosseel, 2012).

2.6 | Statistical analyses

To evaluate our first prediction that size-related traits would generally best predict ANPP but that this would change during environmentally stressful years, we assessed the predictive power of our trait SEMs and how that predictive power changed as function of winter precipitation and annual growing degree days. We first filtered out any SEMs that did not possess a minimum sample size of at least 70 plots due to low trait coverage (12 of 13 SEMs featuring stomatal conductance, all 13 removed for consistency). We then eliminated SEMs that did not converge (i.e. no solution for the global variance–covariance matrix, 3 SEMs) or contained variables with negative variances (i.e. Heywood cases, 13 SEMs). Next, we evaluated several fit measures for each SEM including the χ^2 statistic, the comparative fit index (CFI), the root mean squared error of approximation (RMSEA) and the standardized root-mean squared residual (SRMR). SEMs with χ^2 *p*-values greater than 0.05, CFI scores greater than 0.9, RMSEA less than 0.1, and SRMR value less than 0.08 were interpreted as providing a good fit for the data. Two additional SEMs failed to meet these fit criteria, leaving 112 SEMs with good fit across all traits and years (Appendices S1 and S2).

We then determined which of the SEMs with good fit best explained ANPP in each year by filtering for the trait SEM with the highest R^2 value for ANPP in each year (Figure 3a). Importantly, when selecting the best fitting SEM in each year, we did not compare all 112 SEMs against one another but instead compared different trait SEMs within individual years (e.g. comparing 2008 height SEM vs. 2008 leaf area SEM, not 2010 height SEM vs. 2008 leaf area SEM). For most years, this meant comparing ~10 trait SEMs. Furthermore, our SEMs were not assembled using any step-wise process of parameter or path deletion/insertion, which has been shown to be a problematic because it ignores model selection uncertainty (Mundry & Nunn, 2009; Whittingham et al., 2006). Instead, we kept model structure consistent across traits and years and varied only the identity of the traits used for the CWM and FDis parameters (Figure 2). Model selection approaches with SEMs have been found to be robust to model selection uncertainty, but typically involve the comparison of Akaike information criterion (AIC) or Bayesian Information Criterion (BIC) scores, which estimate overall model fit and parsimony (Garrido et al., 2022; Lin et al., 2017). Here, we focussed our model selection approach on R^2 values for ANPP instead of AIC or BIC scores, as we are interested in the identity of trait SEM that best predicts observed ANPP levels not the trait which provides the best overall model fit across all pathways. Trait SEMs that possessed the highest R^2 value for ANPP in at least 1 year are hereafter referred to as 'best fitting SEMs'. To determine how changing climate influences our ability to predict ANPP, we then performed linear regressions examining how ANPP R^2 values in our best fitting SEMs varied with annual winter precipitation (Figure 3b,c) and annual growing degree days (Appendix S4).

To evaluate our second prediction focussed on mass ratio effects versus niche complementarity effects and how the relative

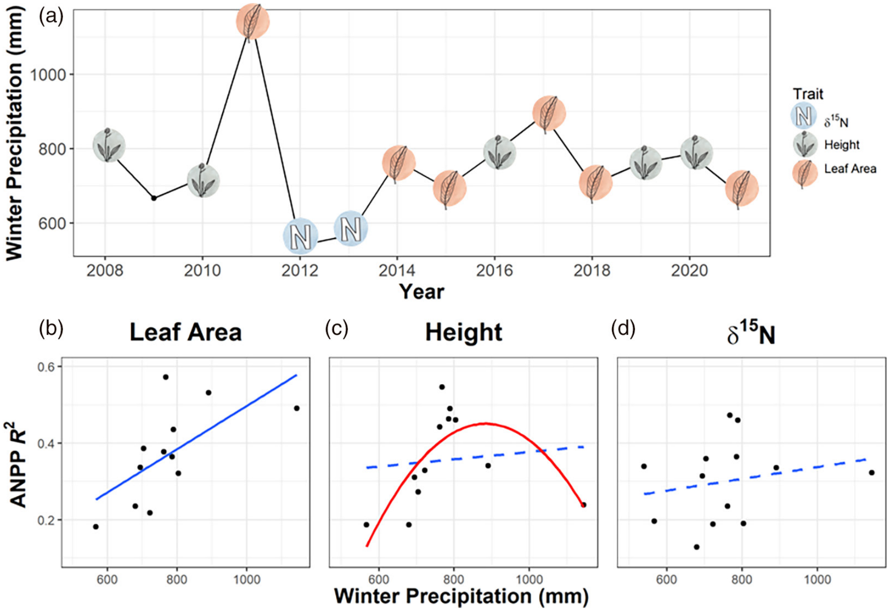


FIGURE 3 (a) Annual winter precipitation (October–May) from 2008 to 2021, shapes show the identity of the trait structural equation model (SEM) which best predicted above-ground net primary productivity (ANPP) in each year. Panel two shows the relationship between ANPP R^2 values and annual winter precipitation for trait SEMs incorporating leaf area (b), height (c), and δ^{15}N (d). Lines of best fit from linear regressions between winter precipitation and ANPP are shown for (b–d). Solid lines indicate a significant relationship while dashed lines indicate a nonsignificant relationship. For height, quadratic linear regression (shown in red) is also included, as this model provided a better fit than simple linear regression.

importance of these functional mechanisms might shift with climatic stress, we examined the path coefficients directly linking CWM and FDis to ANPP in our best fitting SEMs (Appendix S3). Specifically, we performed linear regressions to assess how the strength and magnitude of these path coefficients changed as function of annual winter precipitation (Figure 4a–c) and annual growing degree days (Appendix S4).

To assess our third prediction focussed on how biotic mechanisms versus local abiotic conditions determine ANPP and how the relative importance of these factors might shift with climatic stress, we compared the total effects of biotic mechanisms and local abiotic variables in our best fitting SEMs (Appendix S3). While the total impacts of CWM and FDis on ANPP can be inferred by examining only direct path coefficients, both direct and indirect effects must be considered when determining the total impact of local abiotic variables on ANPP. Indirect effects are calculated by multiplying the path coefficients of two or more direct path coefficients. For example, to calculate the indirect effect of snow-depth on ANPP via CWM, we multiplied the coefficient of the path linking snow-depth to CWM by the coefficient of the path linking CWM to ANPP (i.e. 'snow-depth to CWM to ANPP' = 'snow-depth to CWM' × 'CWM to ANPP'). Total effects are then calculated for each abiotic variable by summing all direct and indirect path coefficients that lead from snow-depth, snow-depth^2 or topography to ANPP. For example, to calculate the total effect of snow-depth on ANPP, we summed all direct and indirect effects of snow-depth on ANPP (i.e. total effects of snow-depth = 'snow-depth to ANPP' + 'snow-depth to CWM to ANPP' + 'snow-depth to FDis to ANPP'). Here, we use both significant and nonsignificant path coefficients in the calculation of total effects to holistically examine the impact of total abiotic effects. Importantly, excluding nonsignificant path coefficients would bias our interpretation by removing years where either direct and/or indirect effects are weak. We then compared the magnitude and sign of each abiotic variable's total effects with the total effects of each biotic mechanism and performed linear regressions to assess how the impact of local abiotic variables changed as a function of annual winter precipitation (Figure 4d–f) and annual growing degree days (Appendix S3).

Finally, to assess our fourth prediction that considering the interaction between annual climatic conditions and biotic/abiotic variables would improve our ability to predict ANPP across time, we analysed our raw data across all years by coupling multimodel inference using linear mixed effects models with variance partitioning. To do this, we built a global linear mixed effects model using the lme4 package (Bates et al., 2014), which featured ANPP as the response variable and trait metrics from our best fitting SEMs (CWM and FDis), abiotic variables (snow-depth, snow-depth^2, slope, aspect, elevation, annual winter precipitation) and interaction effects between each predictor and annual winter precipitation as fixed effects. Additionally, we included year and plot as random factors to

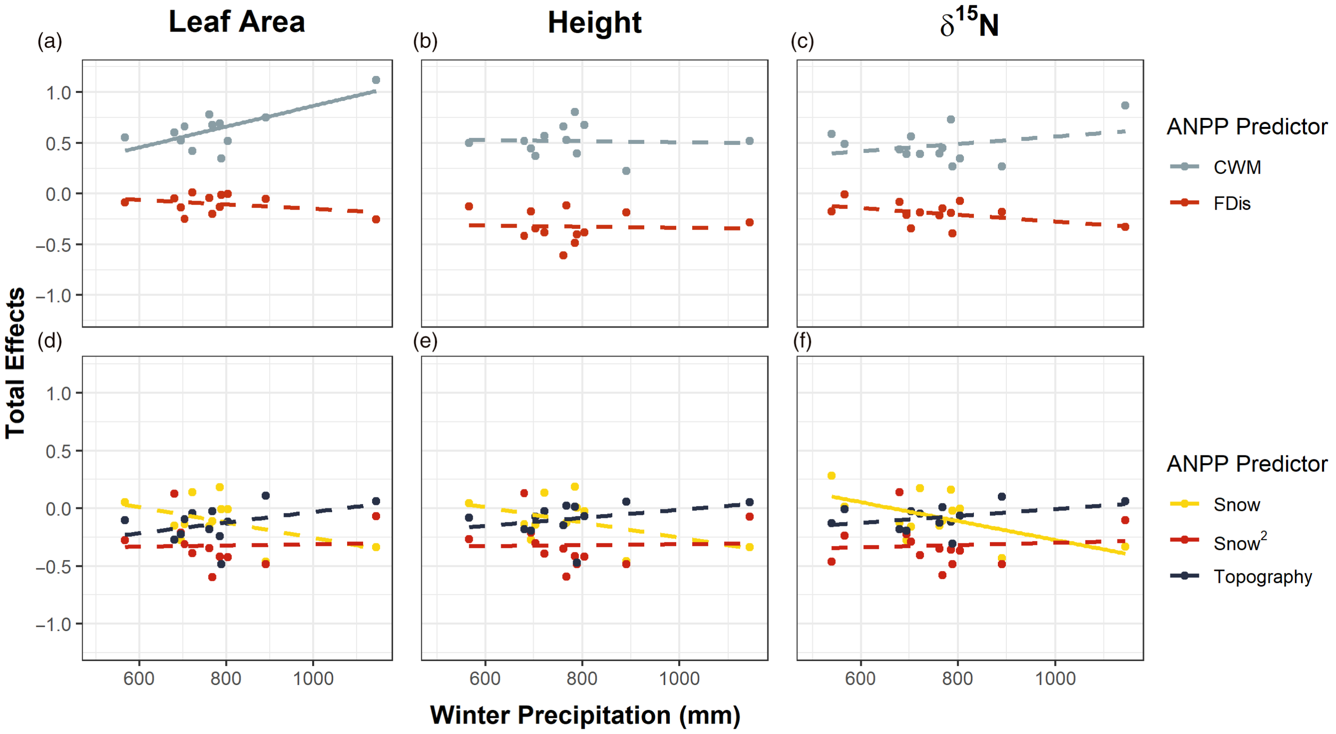


FIGURE 4 Total effects (sum of all direct and indirect path coefficients) of biotic and abiotic predictors on above-ground net primary productivity (ANPP) regressed against annual winter precipitation (mm) for leaf area (a/d), height (b/e), and δ^{15}N (c/f) SEMs. Different colors indicate the specific predictor variable influencing ANPP; total biotic influences (community weighted means and functional dispersion, a/b/c) and total abiotic influences (snow-depth, snow-depth^2, and topography d/e/f) on top and bottom respectively. Solid lines indicate a significant relationship between winter precipitation and ANPP, while dashed lines indicate a nonsignificant relationship.

reflect the fact that each plot was repeatedly sampled across years. Interaction effects with annual growing degree days were not included in the model because neither SEM R^2 values nor individual SEM predictors showed significant relationships with this climate variable during SEM analysis. We then used the 'dredge' function in MuMIn package (Barton, 2020) to create all possible subset models of the global model and ranked these according to AICc score (AIC value corrected for sample size). Next, we selected all models that were within six AICc points of the lowest AICc model (347 models total) and used a model averaging technique known as the 'zero method' to calculate average parameter estimates (Grueber et al., 2011). This method calculates averages by assigning a 0 value to parameters when they are missing from subset models. Once we identified significant predictors, we used the 'partR2' function in the partR2 package (Stoffel et al., 2021) to assess semipartial R^2 values, in other words, the amount of variation uniquely explained by significant effects, for the global model. This approach allowed us to identify how consideration of significant interactions effects between climate and biotic/abiotic variables improved our ability to predict ANPP across time.

3 | RESULTS

3.1 | Best fit SEMs for ANPP

Of the 112 SEMs that met our filtering criteria, at least one SEM in every year exhibited good fit; SEMs featuring nine different traits (δ^{15}N, LDMC, leaf area, height, SLA, percent nitrogen, percent carbon, carbon to nitrogen ratio and chlorophyll content) exhibited good fit in at least 10 years (Appendix S1). The identity of the trait that best predicted ANPP varied across years, with SEMs featuring leaf area, plant height, and δ^{15}N best explaining ANPP in 6, 5 and 2 out of 13 years, respectively (Figure 3a). Other traits did not meet the criterion for best fit and were thus excluded from all analyses discussed below. Importantly, we found that the identity of the trait SEM that best predicted ANPP varied with the amount of annual winter precipitation (Figure 3a). First, we found that leaf area SEMs exhibited good fit in 12 out of 13 years and explained 18.1% to 57.2% of the variation in ANPP (mean = 37.1%). Moreover, we found that ANPP R^2 values in the leaf area SEMs increased with increasing winter precipitation (Figure 3b, $F_{1,10}=7.128$, $p=0.024$, Adjusted $R^2=0.36$) indicating greater explanatory power in years with high winter precipitation. Consequently, leaf area SEMs had the best fit in the two highest winter precipitation years (2011, 2017) and failed to converge in the year with the lowest winter precipitation (2012). Second, plant height SEMs also exhibited good fit in 12 out of 13 years and explained a similar amount of ANPP variation as leaf area SEMs (mean = 35.5%, range = 18.6%–54.6%). However, the relationship between ANPP R^2 values and winter precipitation in these SEMs was non-linear, with explanatory power reaching its maximum in average winter precipitation years and low explanatory power in both low and high winter precipitation years (Figure 3c, quadratic linear regression; $F_{2,9}=6.35$, $p=0.019$, Adjusted $R^2=0.49$). The plant height SEM also failed to converge in the year with the lowest winter precipitation (2012). Finally, δ^{15}N SEMs exhibited good fit in all 13 years but had the lowest average predictive power for ANPP of the three traits (mean = 30.1%, range = 12.8%–47.3%). R^2 values for the δ^{15}N SEMs were not significantly correlated with annual winter precipitation (Figure 3d); however, δ^{15}N SEMs had the best fit in the two lowest winter precipitation years (2012, 2013). No trait SEMs showed significant relationships between ANPP R^2 values and annual growing degree days (Appendix S4).

3.2 | SEM biotic (trait) effects on ANPP

We found that the sign and magnitude of biotic effects inferred from trait-ANPP path coefficients for both CWMs and FDis were consistent among the best fitting SEMs outlined above (Figure 4a–c). All SEMs showed CWM trait values exerting large and positive effects on ANPP (leaf area SEM: mean = 0.64, range = 0.35 to 1.17; plant height SEM: mean = 0.51, range = 0.23 to 0.80; δ^{15}N SEM: mean = 0.47, range = 0.27 to 0.86). In contrast, the influence of FDis values on ANPP was weaker and generally negative (leaf area SEM: mean = 0.10, range = −0.25 to 0.01; plant height SEM: mean = −0.32, range = −0.61 to 0.11; δ^{15}N SEM: mean = −0.19, range = −0.39 to −0.01). We found that some of this variation in the strength of biotic effects (path coefficients) was explained by climatic variation among years. In leaf area SEMs, the CWM ANPP path coefficients showed a significant, positive relationship with annual winter precipitation (Figure 4a; $F_{1,10}=10.58$, $p=0.009$, Adjusted $R^2=0.47$), suggesting a stronger relationship in years with greater winter precipitation. In contrast, leaf area FDis was not significantly related to winter precipitation and neither plant height nor δ^{15}N SEMs showed any significant relationships between biotic effects (either CWM or FDis—ANPP path coefficients) and annual winter precipitation. None of the trait SEMs showed significant relationships between biotic effects and annual growing degree days (Appendix S4).

3.3 | SEM abiotic effects on ANPP

We found that the sign and magnitude of the total effects for each abiotic variable on ANPP (the sum of all direct and indirect path coefficients for topography, snow-depth, and snow-depth^2) were relatively consistent across trait SEMs and years (Figure 4d–f). Across all best fitting SEMs, topography (which significantly positively covaried with slope and elevation, while aspect was not important) exerted weak and typically negative influences on ANPP (leaf area SEM: mean = −0.09, range = −0.47 to 0.06; plant height SEM: mean = −0.13, range = −0.49 to 0.11; δ^{15}N SEM: mean = −0.08, range = −0.31 to 0.10). Snow-depth also exerted weak and typically negative effects on ANPP across all trait SEMs (leaf area SEM: mean = −0.09, range = −0.47 to 0.06; plant height SEM: mean = −0.10, range = −0.46 to 0.18; δ^{15}N SEM: mean = −0.07, range = −0.43 to

0.28). However, in the δ^{15}N SEMs we found a significant negative relationship between the total effect of snow-depth on ANPP and annual winter precipitation (Figure 4f; $F_{1,11} = 5.92$, $p = 0.033$, Adjusted $R^2 = 0.29$). Snow-depth^2 had the largest and most consistently negative effect on ANPP (leaf area SEM: mean = −0.32, range = −0.59 to 0.13; plant height SEM: mean = −0.32, range = −0.60 to 0.13; δ^{15}N SEM: mean = −0.32, range = −0.58 to 0.14). Total effects of snow-depth, snow-depth^2, and topography on ANPP were not significantly predicted by annual growing degree days (Appendix S4).

3.4 | Climatic interaction effects

In our global linear mixed effects model, total fixed effects (R^2_m) explained 22.8% of the variation in ANPP while inclusion of random effects (R^2_c) boosted the variation explained to 54.7%. Multimodel inference revealed that CWM of leaf area ($p < 0.001$), CWM of plant height ($p = 0.04$), FDis of plant height ($p < 0.001$) and snow-depth ($p < 0.001$) were retained as significant fixed effects, with all these factors combining to explain a total of 14.3% of the variation in ANPP and trait metrics alone explaining 13.3%. In addition, interactions between CWM leaf area and annual winter precipitation, as well as snow-depth and annual winter precipitation, were retained as significant, explaining an additional 2.5% of the variation in ANPP. These two interaction effects were retained in all models within the top 6 AICc subset, indicating that models which did not include them received little support. Model coefficients, AICc scores and weights for subset models can be found in Appendix S5.

4 | DISCUSSION

Recent studies demonstrating that functional traits have weak predictive power for ecosystem functions through time (van der Plas et al., 2020) may be the result of temporal variability in the B–EF relationship, where the individual traits, functional mechanisms and abiotic variables that best predict ecosystem functions change with annual variation in climatic conditions. Overall, our results are consistent with the hypothesis that traits are dynamic predictors of ecosystem functioning and our analysis revealed that, in an alpine tundra system, the identity of the trait which best predicted ecosystem function varied with the amount of annual winter precipitation, while the relative importance of the functional mechanisms (CWM vs. FDis) and abiotic variables underlying the B–EF relationship remained largely stable. Moreover, multimodel inference with linear mixed effects models reinforced these results, demonstrating that interactions between climate and biotic/abiotic variables significantly affect ANPP across time. However, including these interactions did not greatly increase our ability to predict ANPP and suggests that, in this system, taking these climatic context dependencies into account only modestly improves our understanding of the B–EF relationship. Taken together, our results suggest that that future B–EF research should consider temporal variability in the B–EF relationship, particularly how the predictive power of individual functional traits and abiotic variables may fluctuate as climatic conditions shift due to climate change or in highly variable ecosystems.

4.1 | Best fit SEMs for ANPP

Our finding that trait SEMs related to plant size (leaf area and plant height) best explained ANPP in 11 of 13 years adds to a growing body of research showing that, across a wide variety of experimental and natural systems, traits related to plant size are often the best predictors of ANPP (Cadotte, 2017; Chiang et al., 2016; Gustafsson & Norkko, 2019; Lavorel & Grigulis, 2012). While leaf area SEMs performed well on average, the predictive power of these SEMs showed a strong relationship with annual winter precipitation (Figure 3b). Since leaf area values reflect a species' ability to maintain water/energy balance (Ackerly et al., 2002; Miller & Stoner, 1979; Parkhurst & Loucks, 1972), a sustained summer snowpack resulting from higher levels of winter precipitation could provide a source of consistent growing season soil moisture, allowing larger-leaved species to achieve higher levels of stomatal conductance and/or photosynthesis (Pattison & Welker, 2014). Thus, in high winter precipitation years, communities composed of large-leaved species would be able to fix more carbon and produce more biomass than normal, exaggerating the already strong relationship between CWM leaf area and ANPP (Figure 4a). Low winter precipitation years may produce the opposite phenomenon, where large leaved species are forced to close their stomata more often due to moisture limitation and thus produce uncharacteristically low levels of ANPP (Bowman et al., 1995; Wentz et al., 2019). This minimizes the normally predictive pathway between CWM leaf area and ANPP, leading to failed model convergence in 2012, the year with the lowest amount of winter precipitation.

In contrast to leaf area SEMs, the predictive power of plant height SEMs was maximized in average winter precipitation years and minimized in both low and high winter precipitation years. In these SEMs, predictive power seemed to change due to small increases in the magnitude of both CWM and FDis effects, where the mean and dispersion of plant height exerted slightly larger magnitude effects on ANPP in average precipitation years (Figure 4b). In low winter precipitation years, marginally lower magnitude CWM and FDis effects may result from moisture limitation reducing ANPP in normally productive plots, a similar mechanism to what we inferred for leaf area SEMs. However, unlike leaf area SEMs, high winter precipitation years also dampened plant height CWM and FDis effects on ANPP. This could result from high winter precipitation leading to a larger, later melting snowpack reducing ANPP in normally productive plots via energy limitation. Thus, height SEMs perform best in average winter precipitation years when neither moisture nor energy are limiting plots where communities have high mean heights and low height dispersion.

In the two years with the lowest amount of winter precipitation (2012 and 2013), the SEMs that best explained ANPP switched from size related traits to δ^{15}N. This suggests that while winter precipitation may control the relationship between size related traits and ANPP via moisture and energy limitation, δ^{15}N trait distributions are shaping patterns of ANPP through a different mechanism, which is not as strongly affected by interannual variation in climate. While the ecological interpretation of δ^{15}N trait values is complex, they are broadly thought to reflect the availability of total nitrogen and variation in nitrogen source (abiotic vs. biotic sources) and have been found to vary along gradients of N availability on Niwot Ridge (Craine et al., 2015; Miller & Bowman, 2002; Spasojevic & Weber, 2021). Since a large fraction of nitrogen in the alpine zone comes from melting snow, long-term patterns of snow deposition set the template for the location and type of nitrogen found across the landscape (Bowman, 1992). Thus, even in years with abnormally high or low winter precipitation, nitrogen availability and source are likely to remain relatively constant. The longer timescale of response for nitrogen availability may be the reason that δ^{15}N SEMs continue to be reasonably predictive of ANPP regardless of annual winter precipitation levels, while the predictive power of height and leaf area SEMs varies more directly with the moisture and energy limitations imposed by fluctuating levels of winter precipitation.

4.2 | SEM biotic (trait) effects on ANPP

In all best fitting trait SEMs, CWMs exerted a large, positive influence on ANPP indicating that communities with high average leaf area, plant height and/or δ^{15}N have the highest levels of ANPP. FDis effects, on the contrary, were lower magnitude and usually negative, indicating that communities that contain a greater diversity of trait values for height, leaf area and δ^{15}N had lower levels of ANPP. Taken together, our results offer partial support for our second prediction and add to a growing body of research demonstrating that mass ratio effects are generally more important than niche complementarity effects in determining individual ecosystem functions (i.e. not multifunctionality), particularly in natural systems (Brun et al., 2022; Cadotte, 2017; Chiang et al., 2016; Fotis et al., 2018; Needham et al., 2022; van der Plas, 2019).

However, the stability of these two functional mechanisms across trait SEMs and temporally varying climatic conditions conflicts with our second prediction that niche complementarity effects would become more important during climatically stressful years. Moreover, this finding contradicts research from experimental grassland and forest systems suggesting that niche complementarity effects tend to exert a more positive impact on ecosystem functions when environmental conditions become harsher (Mori, 2018; Wang et al., 2013; but see Jucker et al., 2016 who found strong spatial but weak temporal B–EF context dependency). This may indicate that niche partitioning among species (i.e. niche differences) is relatively unimportant in determining ANPP in this alpine ecosystem, and instead, ANPP is primarily shaped by the presence of dominant species possessing traits, which provide a competitive advantage (i.e. hierarchical fitness differences) in a specific environmental context (e.g. species with high leaf area trait values, especially in high winter precipitation years; Cadotte, 2017). Alternatively, because our plots are distributed across a fairly large area with high beta-diversity (Spasojevic et al., 2013; Spasojevic & Suding, 2012), differences in CWM and FDis trait values among habitat types could be so large that they mask the positive effects of niche complementarity, which are acting at finer spatial scales. Our cross-community analysis may show negative effects of FDis on ANPP because plots positioned in energy-limited snowbank communities possess high FDis for size-related traits and very low ANPP, while plots in abiotically mild moist meadow communities possess low FDis for size related traits and high ANPP. If instead we were to examine the B–EF relationship at a smaller spatial scale by only using plots within a single alpine community type, the effects of niche complementarity might appear to be positive and relatively more important. For example, facilitation is known to be an important process in dry, wind-swept fellfield communities where dominant cushion plants ameliorate microclimatic conditions for subordinate species (Butterfield et al., 2013; Kikvidze et al., 2015), perhaps generating a positive relationship between functional dispersion and ANPP within this community type.

4.3 | SEM abiotic effects on ANPP

The relatively low magnitude of total effects for abiotic variables in our best fitting SEMs likely results from direct and indirect effects often displaying opposing signs. For example, in leaf area SEMs, the direct pathway linking snow-depth and ANPP was strongly negative, but the indirect pathway through the CWM of leaf area was positive (Appendices S1 and S2). These contradictory effects confirm previous research showing that snow-depth plays an important but complicated role in determining ANPP and species composition (Walker et al., 1993), with high snow-depth values lowering ANPP directly, while simultaneously driving an increase in leaf area CWM values which then have strong, positive knock-on effects for ANPP. This example highlights the usefulness of SEMs for B–EF research, as they are able to disentangle complex relationships, which might be obscured when using other methods like generalized linear modeling or variance partitioning which do not consider indirect effects (Grace et al., 2014, 2016).

Only in the δ^{15}N SEMs did the total effect of an abiotic variable vary significantly with winter precipitation, with snow-depth exerting a negative effect on ANPP in high winter precipitation years but a positive effect in low winter precipitation years. This result suggests that the impacts of snow-depth on ANPP are context dependent. In years when winter precipitation is high, increasing snow-depth likely restricts ANPP by limiting the length of the growing season, while in low winter precipitation years increasing snow-depth boosts ANPP by alleviating moisture limitation. Importantly, this significant trend may only be visible in δ^{15}N SEMs because they are the only SEMs, which converged in all 13 years and possesses a path coefficient value for the lowest precipitation year (2012) in which snow-depth exerted a strong positive effect on ANPP. Overall, our SEMs indicate that local abiotic conditions, particularly snow-depth, play an important and context-dependent role in driving ANPP, but that the combination of strongly opposed direct and indirect effects lead to small total effects.

4.4 | Climatic interaction effects

Multimodel inference using data across all years largely reinforced our conclusions from SEM analysis, with ANPP once again significantly correlated with CWM leaf area, CWM height, FDis height and snow-depth. While δ^{15}N trait metrics did not appear as significant, this is expected given that δ^{15}N SEMs did not perform particularly well at predicting ANPP and only became the model of best fit in 2012 and 2013 due to poor performance for leaf area and height SEMs in the two lowest precipitation years. Furthermore, the two variables we found had context-dependent effects with winter precipitation during SEM analysis, CWM leaf area and snow-depth (in δ^{15}N SEMs), also showed up as significant interaction effects in multimodel inference. However, inclusion of these two interaction effects did not greatly increase our ability to predict ANPP across time, and total fixed effects in the global model still explained much less variation in ANPP than the within-year SEMs (van der Plas et al., 2020). The inability of interaction effects to substantially improve predictive power may result from the fact that this alpine system is composed of hardy, long-lived species which may not quickly respond to annual variation in climatic conditions. While species composition is changing at Niwot and the Rocky Mountains more broadly (Huxley & Spasojevic, 2021), these changes are occurring at the scale of decades (Scharnagl et al., 2019; Spasojevic et al., 2013) and effects on the B–EF relationship may not be clearly visible over the 13-year period of our study. Temporal shifts in the B–EF relationship may be larger in annual communities where species composition can more quickly change in response to local and/or regional changes in climatic conditions, leading to immediate cascading impacts on ecosystem function (Felton et al., 2021; Shaw et al., 2022).

4.5 | Study limitations

Although our results suggest that the explanatory power of the functional traits underpinning ecosystem functions can vary dynamically through time, it is important to acknowledge limitations with our observational approach. First, NWT's Saddle plots do not equally represent the diversity of community types found on Niwot Ridge. Certain community types (e.g. fellfield, $N = 8$ plots; wet meadow, $N = 4$ plots) are under-represented, potentially biasing our interpretations of which traits and mechanisms are most important across the alpine tundra as whole. The low number of fellfield plots is especially problematic given that facilitation and resource partitioning are known to play an important role in this high stress/low-resource community type (Bertness & Callaway, 1994; Butterfield et al., 2013). More data from under-represented community types should be collected so that analyses of the B–EF relationship can be conducted within community types as well as across them. Second, more detailed trait data could improve our ability to explain ANPP across the alpine landscape. Specifically, incorporating temporal changes in intraspecific trait variation could be a major way to improve the power of trait-based approaches for predicting the B–EF relationship through time. Several studies have found that climatic variation can induce large shifts in intraspecific trait values, with subsequent impacts on community-level trait distributions sometimes exceeding the impact of species composition change (Henn et al., 2018; Jung et al., 2014). In this study, we used habitat-specific trait means to capture a degree of spatial intraspecific variation; however, more detailed trait data collection (e.g. measurements in each year) could reveal how temporal intra-specific variation might generate trait–ecosystem function relationships even stronger than those reported here.

5 | CONCLUSION

In our alpine tundra system, productivity was generally best explained by traits related to plant size (leaf area and plant height); however, this trend changed during low winter precipitation years when δ^{15}N instead best predicted productivity. Without exception, productivity was better explained by the community average values of these traits rather than their variation, suggesting that, while both mechanisms operate simultaneously, mass ratio effects are relatively more important than niche complementarity in determining productivity in this system. The total effects of local abiotic variables on ANPP were relatively small; however, this was due to complex and contradictory direct and indirect (via trait composition) effects. Lastly, some biotic and abiotic variables showed context dependent relationships with winter precipitation, and consideration of these climatic context dependencies marginally improved our ability to predict ecosystem function through time. Taken together, our results suggest that consideration of temporal variation in environmental conditions and the dynamic nature of trait–environment relationships can improve our understanding of the biodiversity–ecosystem function relationship.

AUTHOR CONTRIBUTIONS

Jared D. Huxley lead the writing and analysis. Marko J. Spasojevic collected trait data and contributed to writing and analysis. Caitlin T. White contributed to writing and analysis. Soren E. Weber collected data and contributed to writing. Hope C. Humphries collected the majority of the data.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data used in our analyses are available via NWT LTER's portal on the Electronic Data Initiative website as follows. Saddle precipitation: https://doi.org/10.6073/pasta/b78fc5dbec3fcdfe4a53a009fce2e13d (White et al., 2023a); Saddle temperature: https://doi.org/10.6073/pasta/d3460079bb2cb633f994a2f4075049ef (White et al., 2023b); Saddle snow-depth: https://doi.org/10.6073/pasta/9a1f33fdc75e3ec0c3ac4fe79081f749 (Walker, 2022); Saddle species composition: https://doi.org/10.6073/pasta/1b4e85930251df1eba3d417fd4f6cd04 (Walker, Humphries, et al., 2022); plant functional traits: https://doi.org/10.6073/pasta/1a06bcffa07e7aa2a4b674af4c427860 (Spasojevic et al., 2022); Saddle aboveground net primary productivity: https://doi.org/10.6073/pasta/56491d9a56214ca7d7f3f26487faf510 (Walker, Smith, et al., 2022). Please check the reference section for data package citations. R scripts used for analysis are available on Zenodo: https://doi.org/10.5281/zenodo.8303140 (Huxley, 2023).

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SUPPORTING INFORMATION

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

Appendix S1. Sample-size and model fit metrics for all structural equation models demonstrating good fit.

Appendix S2. Structural equation models diagrams.

Appendix S3. Effect magnitude and sign for direct, indirect, and total effects of each predictor variable on ANPP for all SEMS demonstrating good fit.

Appendix S4. Analogues of Figures 3 and 4 but examing trends related to growing degree days instead of winter precipitation.

Appendix S5. Summary of subset models generated from global linear mixed effects model.

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