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ARTICLE

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Temporal variability and predictability predict alpine plant community composition and distribution patterns

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Abstract

One of the most reliable features of natural systems is that they change through time. Theory predicts that temporally fluctuating conditions shape community composition, species distribution patterns, and life history variation, yet features of temporal variability are rarely incorporated into studies of species–environment associations. In this study, we evaluated how two components of temporal environmental variation—variability and predictability—impact plant community composition and species distribution patterns in the alpine tundra of the Southern Rocky Mountains in Colorado (USA). Using the Sensor Network Array at the Niwot Ridge Long-Term Ecological Research site, we used in situ, high-resolution temporal measurements of soil moisture and temperature from 13 locations ("nodes") distributed throughout an alpine catchment to characterize the annual mean, variability, and predictability in these variables in each of four consecutive years. We combined these data with annual vegetation surveys at each node to evaluate whether variability over short (within-day) and seasonal (2- to 4-month) timescales could predict patterns in plant community composition, species distributions, and species abundances better than models that considered average annual conditions alone. We found that metrics for variability and predictability in soil moisture and soil temperature, at both daily and seasonal timescales, improved our ability to explain spatial variation in alpine plant community composition. Daily variability in soil moisture and temperature, along with seasonal predictability in soil moisture, was particularly important in predicting community composition and species occurrences. These results indicate that the magnitude and patterns of fluctuations in soil moisture and temperature are important predictors of community composition and plant distribution patterns in alpine plant communities. More broadly, these results highlight that components of temporal change provide important niche axes that can partition species with different growth and life history strategies along environmental gradients in heterogeneous landscapes.

KEYWORDS

alpine vegetation, community composition, fluctuation, Long-Term Ecological Research, Niwot Ridge, predictability, species distributions, temporal variation, variability

INTRODUCTION

Understanding how environmental factors shape species distributions and abundance patterns is a long-standing goal in ecology that has become increasingly relevant to predicting species responses to climate change (Taheri et al., 2021; Thuiller et al., 2008). A large body of research has demonstrated that species ranges can often be predicted by average environmental conditions (Beaumont et al., 2005; Elith et al., 2006), with the magnitude and patterns of temporal variability in those conditions remaining relatively unexplored. However, we know that one of the most salient features of natural systems is that they fluctuate through time. For example, seasonal shifts in precipitation influence resource availability in aquatic systems (Aguilera et al., 2019) and are a key determinant of water availability in water-limited systems like grasslands (Munson et al., 2022). Temperatures in desert systems can swing by as much as 40°C within a single day at any time of year (Hastings et al., 2005), while temperate zones experience lower diurnal variation but greater seasonal changes in temperature (Davidson et al., 1998). Despite clear differences in the magnitude and patterns of temporal variation at multiple spatial scales, the role that spatial heterogeneity in temporal variability plays in shaping species distribution patterns and community structure is rarely tested. As climate change brings more variable and extreme climate conditions (Gulev et al., 2021), understanding how temporal variability in temperature and precipitation patterns shapes species distribution and abundance patterns is increasingly important for and relevant to conservation and management practices.

While community ecologists have considered how the magnitude of temporal variation influences community dynamics (Arellano et al., 2016; Herben et al., 1995), less attention has been directed toward how different patterns of variability shape populations and communities (Sheldon & Dillon, 2016). Today, *in situ* sensors that accurately measure fine-scale spatial and temporal variability in environmental conditions make it possible to accurately quantify these patterns at resolutions (e.g., multiple measurements per hour, multiple locations within a site) that cannot be captured at coarser spatial scales. Temporal variability can be decomposed into two components: the magnitude of variation in environmental factors and the predictability of that variation. While variability characterizes the range of conditions that occur over a given time frame (measured as the CV or variance, for example), predictability describes the extent to which current conditions provide reliable information about future conditions (Moran, 1992; Ruokolainen et al., 2009). Predictability can arise from temporal autocorrelation in the variable of interest (e.g., declining temperatures in autumn), or from a correlation between a cue and future conditions (e.g., changing daylength as a cue for seasonal change) (Bernhardt et al., 2020). In either case, a correlation of 1 represents an environment that is perfectly predictable and a correlation of 0 represents complete unpredictability.

Variability and predictability can provide independent axes for specialization and niche differentiation because each axis has the potential to vary independently from one another and the mean (Botero et al., 2015; Nadeau et al., 2017). The same magnitude of variability can fluctuate stochastically (and thus unpredictably) or be autocorrelated through time, where the conditions at one point in time predict conditions in the future. Furthermore, environmental conditions might exhibit different patterns of variability and predictability at different timescales (Keitt & Fischer, 2006; Mallet et al., 2020). For example, soil moisture may vary unpredictably throughout the day depending on precipitation events, temperature, and solar exposure (Griffin-Nolan et al., 2021). However, over longer timescales, soil moisture patterns may be more predictable due to consistent shifts in temperature and precipitation within or among years (Nippert et al., 2006). Finally, the extent to which an organism perceives environmental change as "fast" or "slow" will depend on its developmental patterns, growth rate, generation time, and life history; for example, a 24-h shift in soil moisture may be a relatively slow change for a microbe and abrupt for a long-lived perennial plant (DeWitt & Scheiner, 2004; Rosenheim & Tabashnik, 1991).

From an evolutionary perspective, life history theory predicts that the rates and patterns of variability and predictability favor strategies for growth and reproduction that, in turn, are likely to influence where species occur and how they interact with other organisms (Nadeau et al., 2017; Orzack, 1985; Tuljapurkar, 1989). Variable and unpredictable environments are expected to favor more conservative, bet-hedging life histories, particularly when environmental changes are relatively rapid in comparison with organismal lifespans; these "jack-of-all-trades, master-of-none" phenotypes may exhibit fixed growth and reproductive patterns that increase their ability to persist under poor conditions at the cost of optimizing performance under favorable conditions (Gremer, 2023; Philippi & Seger, 1989). In contrast, predictable variation can favor adaptive phenotypic plasticity, where organisms use reliable cues to "match" their phenotype or life history patterns to the current or predicted environment (Botero et al., 2015; Nadeau et al., 2017; Scheiner, 1993). Plasticity can unfold in different ways across ontogeny, such as when a cue that an organism experiences early in life sends it down a particular developmental trajectory, or over days or even minutes when regulated by physiological and/or behavioral responses (e.g., acclimation, thermoregulation, metabolic shifts) (Nadeau et al., 2017). Species with "fast" or acquisitive resource use strategies are often able to take advantage of resource shifts through phenotypic plasticity. Given that the prevalence of conservative ("slow") versus acquisitive ("fast") strategies will influence the rates of resource uptake and population growth rates within communities (Rollinson & Brooks, 2007; Ryser & Eek, 2000), species' responses to temporal variation should influence (and be influenced by) interactions with other species (Chesson, 2000). In spite of these broad theoretical predictions, the biological effects of environmental variability and predictability at different timescales have rarely been systematically measured and compared (Dillon et al., 2016), limiting our understanding of how different growth and life history strategies respond to different rates of temporal variability and their impacts on population and community dynamics.

Alpine ecosystems are particularly well-suited for studying how spatial variation in the components of temporal variability influences species distributions and community composition. The topographic complexity of the alpine environment generates considerable microclimatic heterogeneity within and across growing seasons and across space. Within a single landscape, changes in microtopography, slope, and aspect influence exposure to solar radiation and wind (Löffler & Pape, 2020; Seastedt et al., 2004), which in turn drive patterns of snow accumulation (Holtmeier & Broll, 1992; Pérez, 1998; Taylor & Seastedt, 1994). Snow insulates soil during the winter and provides a steady, predictable source of early-season soil moisture as it melts (Schneider et al., 2020). Areas with little snow experience colder, more variable temperatures during the winter and rely on rainfall for water during the growing season (Zhao et al., 2022). In the summer, solar radiation warms and dries exposed soils, while soils that are more sheltered from the sun remain wetter and cooler (Bertoldi et al., 2010). Overall, the heterogeneous topography of the alpine landscape generates a diverse set of habitats that differ in the temporal variability and predictability in the environment that plants experience. Previous work has characterized how differences in average moisture and temperature align with alpine plant community composition (e.g., Litaor et al., 2008), but the effects of temporal variability and predictability in shaping alpine plant communities have not been explicitly investigated.

In this study, we evaluated the roles of variability and predictability in soil moisture and temperature in driving plant community structure and species distribution patterns in the alpine tundra of Niwot Ridge, CO. Using high-resolution, multi-year time series measurements of soil moisture and temperature that are co-located with annually surveyed vegetation plots, we asked two questions: (1) Do temporal variability and predictability predict patterns in plant community composition each year that are not explained by the average conditions alone? (2) How does spatial variation in temporal variability and predictability shape the distributions and abundances of individual species across heterogeneous alpine terrain? We addressed each of these questions considering two different timescales of temporal fluctuations: daily (24-h) and seasonal (early to late summer). We predicted that spatial heterogeneity in the rate (daily vs. seasonal), magnitude (variance), and pattern (predictable vs. unpredictable) of temporal variability would significantly predict community composition and species distribution patterns because stable, predictably variable, and variable but unpredictable environments should select different growth and life history strategies from the species pool. We expected daily variability in soil temperature and seasonal predictability in soil moisture to be particularly important drivers of plant community composition and species distributions in the alpine tundra because spatial heterogeneity in snow accumulation influences diurnal temperature variation during the winter and snowmelt during the growing season. The same rationale led us to expect that species would vary in the extent to which they associate with variable and/or unpredictable environments, consistent with our overarching hypothesis that these two components of temporal variability provide important niche axes that structure communities and drive species distribution patterns in heterogeneous landscapes.

METHODS

Study site

This study used plant and environmental data collected at the Niwot Ridge Long-Term Ecological Research (LTER) site in the Colorado Front Range of the Southern Rocky Mountains northwest of Denver, Colorado (40°03′ N, 105°35′ W). The site extends to the Continental Divide, with an average elevation of ~3500 m above sea level (asl). The mean daily temperature is −8.8°C in winter and −0.5°C in summer, and roughly 80% of the ~1035-mm mean annual precipitation falls as snow (Bjarke et al., 2021; Bowman & Seastedt, 2001; Jennings et al., 2019). Strong and predominantly westerly winds interact with topographic variation to create an unequal distribution of snow across the alpine landscape (Badger et al., 2021;

Hoover et al., 2014; Olyphant & Isard, 1987), which in turn causes spatial variation in soil temperature throughout the year and soil moisture during the growing season. The vegetation at the site is characteristic alpine tundra of the Central and Southern Rocky Mountains, dominated by long-lived herbaceous forbs and graminoids such as *Geum rossii*, *Trifolium parryi*, *Kobresia myosuroides*, and *Deschampsia cespitosa*. The growing season ranges from 1 to 3 months (June–August), depending on topographic position and snowpack.

The Niwot LTER Sensor Network Array is a network of instrumentation that was established in the Saddle Catchment of Niwot Ridge in the summer of 2017 to measure spatial and temporal environmental variation within a single alpine catchment area. The Sensor Network Array consists of 16 permanent towers and associated instrumentation distributed throughout a drainage that spans from the Saddle of Niwot Ridge (3528 m asl) into the upper Green Lakes Valley watershed (Figure 1A), a 0.6-km^2 area located 5.6 km east of the Continental Divide (Bjarke et al., 2021). The towers were placed to span the range of hydrological, topographic, and vegetative variation that exists within the catchment. Each tower is equipped with a Campbell CR1000 data logger that is connected to soil moisture and soil temperature sensors that collect volumetric soil moisture and soil temperature measurements, respectively, every 10 min at 5- and 30-cm depths in a 1-m^2 plot that is placed immediately adjacent to the tower (Figure 1B). Two additional permanent 1-m^2 plots were established immediately downslope from each tower, along existing hydrological pathways, to monitor plant community composition at each node on an annual basis. For the purposes of this study, we considered the "node" as the spatial unit of replication, with the two vegetation plots representing the plant community associated with each node (within ~6 m).

Data collection

We used the first four complete years of soil moisture, soil temperature (Morse & Niwot Ridge LTER, 2022), and vegetation (Reed et al., 2022) data collected from 13 of the 16 nodes in the Sensor Network Array (2018–2021). One node (no. 18) was excluded because it was relocated partway through the study period, another (no. 21) was removed because the soil moisture sensors were not well-aligned with the vegetation plots due to local microtopography, and a third (no. 15) was excluded because of large amounts of missing environmental data due to sensor failure. The first year (2018) of vegetation data from node no. 17 was also excluded due to sensor malfunction, but the remaining years were included. While the sensors in the network array are generally reliable and robust, the harsh alpine environment can take its toll on this equipment, resulting in short gaps in the otherwise continuous data ranging from a few hours to several days. In the 13 nodes we included in our analysis, these gaps usually constituted less than ~3% of any soil moisture and temperature data series. We employed two methods to fill the gaps that did occur in the data. For the temperature data, we used the R package MICE (Multiple Imputations by Chained Equation), a technique commonly used for this type of data (van Buuren & Groothuis-Oudshoorn, 2011). For the moisture data, we used the R package "mtdsi" to fill in data where there were small gaps (100 min or less) in the time series (Junger & Ponce de Leon, 2018). Both methods leverage data from different time points at the same location and different locations at the same time point to estimate missing values.

Vegetation surveys in the Sensor Network Array at Niwot Ridge have been conducted on an annual basis at peak productivity since 2018; in this study, we use the data from the first four surveys (2018, 2019, 2020, and 2021). The point-intercept sampling method was used for each survey (Spasojevic et al., 2013). The sampling protocol is summarized in detail in the metadata for the published data set (Reed et al., 2022). Briefly, each year we sampled 100 locations in each 1-m^2 plot in a uniform grid with 10 cm $\times$ 10 cm spacing. At each of the 100 locations, a metal pin flag was inserted vertically through the vegetation to the soil surface, and each species that touched the pin at that location was recorded. We did not count multiple touches from the same species at a single grid position, as it was often difficult to distinguish between one individual versus multiple individuals of the same species. After all 100 locations were sampled in a plot, we conducted an exhaustive search of the plot to identify and record any other species that were present but never touched by a pin. This procedure provides robust estimates of species abundance, total composition, and the presence or absence of rare species in each plot. In 2018, we conducted vegetation surveys in one 1-m^2 plot at each node; from 2019 onward, we collected data in both permanent plots at each node (Figure 1B) to better characterize the vegetation community of each node. See Appendix S1: Table S2 for summary statistics by species.

We used the plant survey data to evaluate the relationships between temporal variability in the environment and the distribution and abundance of alpine plants in the Sensor Network Array. To evaluate the distribution of species, we calculated the occurrence (1 for present, 0 for absent) of each species in each plot by comparing the list of species that had been found in

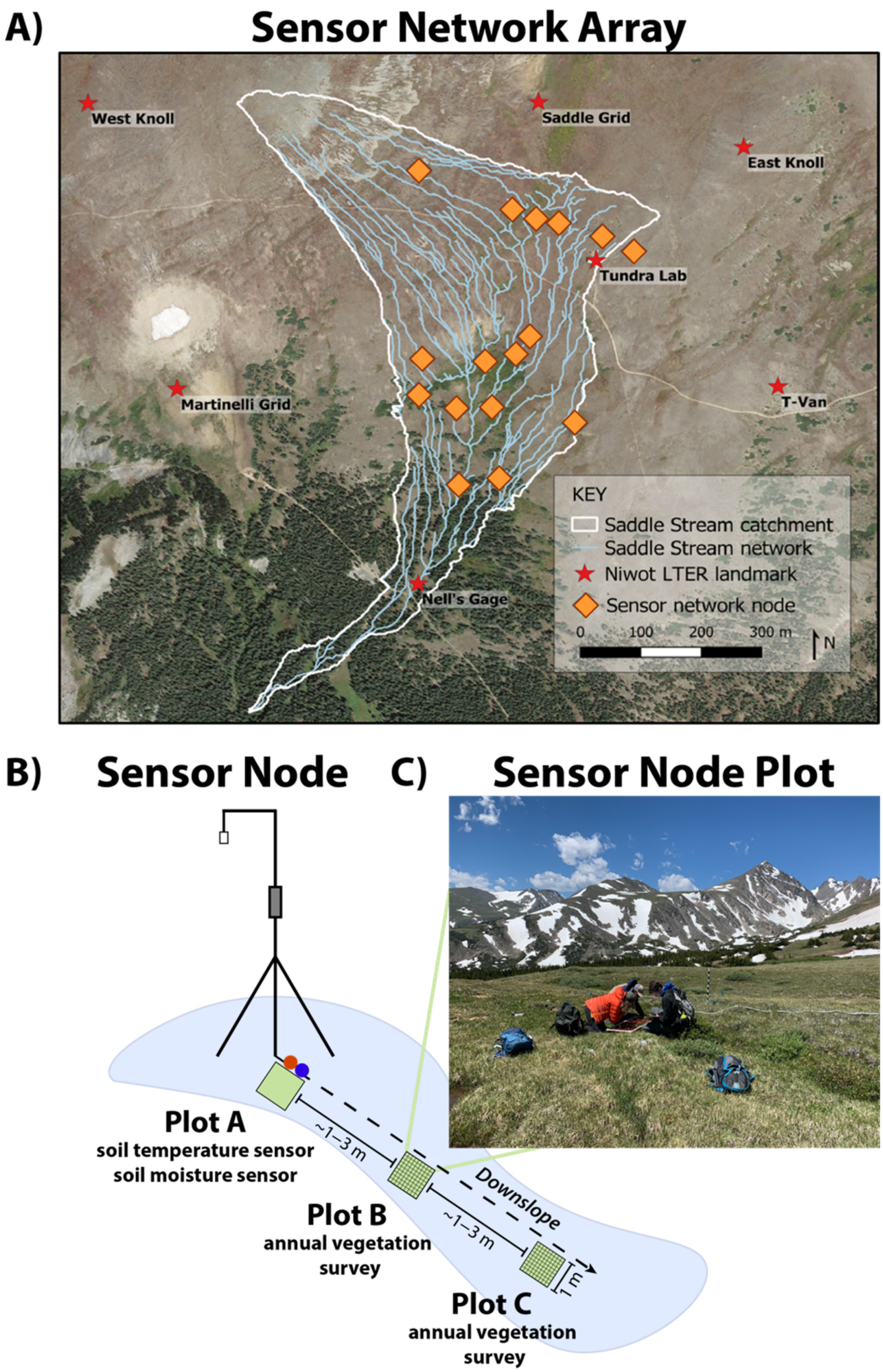

FIGURE 1 Spatial arrangement of nodes, sensors, and vegetation plots in the Sensor Network Array of the Niwot Ridge Long-Term Ecological Research (LTER) site. (A) The Niwot Ridge Sensor Network Array consists of 16 nodes (orange diamonds) distributed throughout a 45-ha catchment from the Saddle of Niwot Ridge to the subalpine zone of the Green Lakes Valley. Thirteen of the 16 nodes had sufficiently continuous data sets to be included in this study. (B) Each node in the array consists of a single tower with three permanently marked 1-m^2 plots (green squares) placed along existing water flow paths downslope from the tower. Plot A is adjacent to the tower and is equipped with soil moisture (blue circle) and soil temperature (red circle) sensors that collect measurements at 5- and 30-cm depths every 10 min. Plots B and C are permanent monitoring plots that are approximately 1–3 m apart following the path of natural water movement. The vegetation plots are surveyed every year at peak biomass for plant community composition using point-intercept sampling at 100 evenlyspaced positions within the plot (indicated by hatching). In this study, we used soil temperature and moisture data from Plot A and plant community data from Plots B and C to evaluate community composition and species associations with temporal variability in soil moisture and temperature at each node. (C) A photograph of an annual vegetation survey at one of the plots in the Sensor Network Array. Photo credit: Nancy C. Emery.

a plot to the list of all species found across all plots. We calculated the total abundance of each species in each plot by counting the number of grid locations where it was touched by a pin (with a maximum of one touch per grid position giving an abundance of 100 in a plot). Species that were found in the plot but never contacted by a pin were given a value of 0.5 (i.e., less than one). We did not normalize abundances to the total number of touches across all species to ensure that we captured differences in the absolute abundances of species across plots. In 2018, abundances were calculated from only one plot per node (ranging from 0.5 to a maximum possible value of 100); in 2019–2021, when two plots were sampled per node, we summed the abundances across plots to obtain a single value per node, so the total possible range of abundance for a species was 0.5–200. Year was included as a fixed effect in the analyses (see below) to account for the differences in the number of plots sampled per node each year.

Data analysis

All analyses in this study were conducted in R version 4.3.3 (R Core Team, 2024), and all code is archived on Zenodo at https://doi.org/10.5281/zenodo.13629151.

The first step in our analyses was to identify biologically meaningful ways to describe the mean, variability, and predictability in soil moisture and temperature at different timescales. We used year-round soil temperature data because both growing season and winter temperatures influence tundra plant community composition (Niittynen et al., 2020; Suding et al., 2015). We restricted our analysis of soil moisture to days where the ground was not frozen (temperature > 0°C, generally late April to late September or early October), which is when it influences plant growth and reproduction (Taylor & Seastedt, 1994). Using these time windows, we calculated mean annual soil temperature at each node as the average of all measurements each year, and the mean annual soil moisture as the average moisture when the soil temperature was >0°C each year.

We calculated variability in two different ways that represented two different timescales. First, to quantify variability within a typical day (i.e., within a 24-h period, hereafter referred to as the daily timescale), we used all temperature from the sensor network to calculate the average daily CV in soil moisture and soil temperature at each node for each year. Second, we described variability over each growing season (hereafter the seasonal timescale) using the number of times soil temperature or moisture measurements crossed physiologically important thresholds. The use of threshold crossings over the season, rather than the CV or other summary statistics, recognizes that the effects of seasonal fluctuations on plant growth and survival depend largely on their relationship with the mean, and in particular the potential for fluctuations to push plants beyond discrete physiological limits. For example, soil moisture fluctuations during a dry part of the season will induce episodes of drought stress that impact growth, survival, and reproduction, while fluctuations of the same magnitude will have little to no effect on plants when water is readily available and abundant. We used thresholds of 0.4°C and 13% volumetric water content (VWC) for soil temperature and moisture, respectively, based on published literature that documented these are critical thresholds for alpine plants (Billings & Bliss, 1959; Nagelmüller et al., 2016). Thus, seasonal soil temperature variability was calculated as the number of times the temperature at each node went above or below 0.4°C in a year (Nagelmüller et al., 2016, 2017). For moisture, we calculated the number of times the soil moisture level crossed 13% VWC (Billings & Bliss, 1959) during the growing season.

We represented the predictability of environmental conditions using the autocorrelation factor (ACF), which measures the average correlation between past and future time points over a defined interval (Nounou & Bakshi, 2000). For daily predictability, we calculated the average ACF in hourly average values measured 1 day (24 h) apart, for every hour of the day and all days in the year (for temperature) or growing season (for soil moisture). Seasonal predictability was calculated as the average ACF among daily average values with a lag of 60 days for all pairs of points that could be computed within the year (for temperature) or growing season (for soil moisture). We chose 60 days because this time frame spanned enough of the growing season to characterize how well early-season conditions predicted late-season conditions and maximized the variation in ACF values detected among nodes.

We examined the correlations among the mean, variability, and predictability in soil moisture and temperature at each timescale (Appendix S1: Figures S1 and S2). While we found some significant cross-correlations among variables, we decided to include all variables given their potential biological importance while recognizing our limited ability to isolate the direct effects of variables that are correlated (see below).

Community associations with variability and predictability

We used redundancy analysis (RDA) to examine how plant community variation among node communities in the Sensor Network Array relates to environmental variables. RDA is an asymmetric constrained ordination method (Zuur et al., 2007) that models the relationship between a predictor matrix and a response matrix (Legendre & Legendre, 2012). After performing a regression between matrices, RDA uses principal components analysis (PCA) to reduce the dimensionality of the predicted relationships into canonical axes that represent linear combinations of the explanatory variables (Legendre & Legendre, 2012). We used this approach to quantify relationships between environmental matrices containing our environmental variables (the predictor matrix) on plant community composition (the response matrix) and visualize the multivariate relationships between them. Due to the size of our data set ($N = 13$ nodes, 4 years), we were not able to consider nonlinear relationships between environmental axes and community composition, and acknowledge this as a limitation of this approach (Legendre & Legendre, 2012; Zuur et al., 2007). Prior to the RDA, we first tested for spatial autocorrelation in the environmental variables across the Sensor Network Array using a Mantel test (Mantel, 1967). We found weak correlations in all comparisons (soil temperature variability: $r = 0.09$, $p = 0.14$; soil temperature predictability: 0.12, $p = 0.09$; soil moisture variability: $r = 0.07$, $p = 0.21$; soil moisture predictability: 0.11, $p = 0.12$), so we did not incorporate the distances among nodes in our RDA.

We developed three different models to evaluate the relationships between community structure and our environmental variables using RDA. All RDA models were implemented using the R package Vegan (v.2.6-4). The first model included only the annual mean conditions in soil moisture and soil temperature and fixed effects of year and node (the RDA does not allow random effects). The second included daily measures of variability (CV) and predictability (autocorrelation) for soil moisture and soil temperature in addition to the annual mean, year, and node. The final model included our measures of seasonal variability (threshold crossing) and predictability (autocorrelation) for soil moisture and soil temperature, annual means, year, and node. In all models, we determined the importance of the mean, variability, and predictability of soil temperature and moisture in driving community structure by evaluating their relative contributions to the total explained variance and the statistical significance of each environmental term. We also investigated the correlations between environmental variables and the constrained axes of variation to determine which variables were most important. Finally, we used the adjusted R^2 values of each RDA to compare the total variation explained by different models; these comparisons were most relevant for the models that contained the same number of explanatory variables.

Species associations with variability and predictability

To examine the variation among species in their associations with temporal variation over both daily and seasonal timescales, we modeled patterns of species occurrence (presence/absence) and abundance (total number of "touches") against each of our environmental variables using mixed-effects models (LME4 package, Bates et al., 2015). Each model contained fixed effects of year ($N = 4$) and one environmental variable (e.g., mean soil temperature, daily variability in soil moisture, etc.), and a random intercept term for each node ($N = 13$) to account for repeated measurements at each location. We included random intercepts and slopes for each species to test whether species ($N = 87$) had different relationships with each environmental variable. Models that included multiple environmental predictor variables did not converge, likely due to the limited number of independent replicates in the data set ($N = 13$ nodes), even with 4 years of sampling. Consequently, we proceeded with models that evaluated one predictor variable at a time, which included the appropriate random effect structure but could not account for correlations among predictors. We present the pairwise correlations between predictors in Appendix S1: Figures S1 and S2, respectively, so they can be considered in association with the results of these analyses. While this approach is conservative and may have low statistical power for less common species, the spatial scale and exceptional time resolution of the environmental data nonetheless provide a unique opportunity to evaluate relationships between temporal variability and species distribution and abundance patterns.

We modeled occurrence using logistic regression to accommodate the binary nature (presence/absence) of the occurrence data. We used all the full vegetation data set in the occurrence analysis, assigning each species a value of "0" if absent and "1" if present at each node.

We modeled abundance using a regression with a zero-truncated Poisson distribution and an observation-level random effect (OLRE) to account for overdispersion (Appendix S1: Table S2). We excluded species absences (i.e., plots where a species abundance = 0) and rounded values that were not integers (e.g., 0.5) up to the nearest integer to align with the expectations of count data. While a Poisson model is most appropriate for count data, we compared the fit and results of models that assumed a Gaussian binomial (considering "touches" as presence/absence data) and a negative binomial (to account for overdispersion in the Poisson) distribution. These models did not provide better fits to the data and, in some cases, failed to converge, yet overall provided qualitatively similar results to the Poisson model.

We tested whether species exhibit significant variation in their relationships (i.e., occurrence and abundance patterns) with the mean, variability, and predictability of soil moisture and temperature by first examining how many species had nonzero slope estimates (95% CI around the median does not overlap zero, as determined by nonparametric bootstrap) (R MASS package, Venables & Riplen, 2002). Note that 95% confidence intervals could overlap zero because there was no relationship between the predictor variable and the occurrence or abundance of a species or because we did not have sufficient power to detect a relationship, with the latter being particularly relevant for taxa that were rare in our data set. However, this should not bias comparisons among environmental predictors as they are based on the same response variables. We also compared the amount of variation explained by the random effects structure (conditional R^2) in the variability/predictability models and models with mean environmental covariates, and in models that included random intercepts for species without random slopes. To highlight some of the contrasting relationships with variability and predictability that we detected among species, we visualized the predicted slopes for a subset of six taxa that were abundant in our data set and represent a range of habitat types and functional groups in the alpine tundra plant community at Niwot Ridge: *G. rossii* (widespread forb), *Carex scopulorum* and *D. cespitosa* (common moist meadow graminoids), *K. myosuroides* (common dry meadow graminoid), *T. parryi* (widespread forb legume), and *Sedum lanceolatum* (widespread succulent). The names, total occurrences per node and per plot, and average plot-level abundance for all 87 taxa are provided in Appendix S1: Table S1.

RESULTS

Community associations with variability and predictability

Mean soil moisture and temperature explained a relatively small but statistically significant amount of the variation observed in the alpine plant community among nodes in the Sensor Network Array over the 4 years of this study (RDA, adjusted $R^2 = 10.4\%$, $p = 0.001$) (Figure 2A). The first and second RDA axes explained 10.5% ($p = 0.001$) and 3.6% ($p = 0.027$) of the total variation in community composition, respectively. The first RDA axis was primarily correlated with mean soil moisture ($r = 0.98$ for soil moisture and $r = -0.46$ for soil temperature), while the second RDA axis was primarily correlated with soil temperature ($r = 0.17$ for soil moisture and $r = 0.88$ for soil temperature). Individually, mean soil moisture explained 10.2% of the variation in community composition ($p = 0.001$) while mean soil temperature explained only 3.8% ($p = 0.031$).

Daily variability and predictability in soil moisture and temperature substantially increased the amount of variation in community composition explained by the model, even after adjusting for the number of predictors. In the RDA that included mean, daily variability, and daily predictability in soil moisture and temperature as predictor variables, all axes had an adjusted R^2 of 27% ($p = 0.01$). The communities are separated along a variable-to-invariable axis (RDA1) and a hot/dry-to-cold/wet (RDA2) axis (Figure 2B). The first RDA axis explained 17.4% of the variation in community composition while the second explained 8%. Mean soil moisture and the variability in soil moisture and temperature were the most correlated with the first RDA axis ($r = 0.67$, -0.95, and -0.74, respectively), while the second RDA axis was primarily associated with mean conditions in soil moisture and temperature ($r = 0.48$ for both variables). Mean soil moisture had the largest explanatory power of any term in the model (10.2% of variation explained, $p = 0.001$), followed by daily variability in soil moisture (8.8%, $p = 0.001$). In contrast, daily variability in temperature explained more variation (7.3%, $p = 0.001$) than mean temperature (3.8%, $p = 0.008$). Daily predictability in soil moisture (3.2%, $p = 0.02$) explained a relatively small amount of the variation in community composition, while daily predictability in soil temperature had the lowest explanatory power of any term (2.6%, $p = 0.08$).

Seasonal variability and predictability also improved the explanatory power of differences in community composition over the model with means alone (adjusted $R^2 = 21\%$; $p = 0.001$). The environmental variables separated the vegetation in the Sensor Network Array plots along a hot/dry-to-cold/wet axis and a variable/unpredictable-to-invariable/predictable axis (Figure 2C). The first and second RDA axes explained 15.9% and 6.8% of the total variation, respectively. The first axis was most correlated with mean ($r = 0.71$), variability ($r = -0.99$), and predictability ($r = 0.80$) in soil moisture, while the second axis was most associated with the mean ($r = 0.42$) and variability ($r = 0.57$) in soil temperature. Variability in soil moisture explained almost as much variation in community composition as mean soil moisture (9.8% of variation explained, $p = 0.001$ compared to 10.2%, $p = 0.002$).

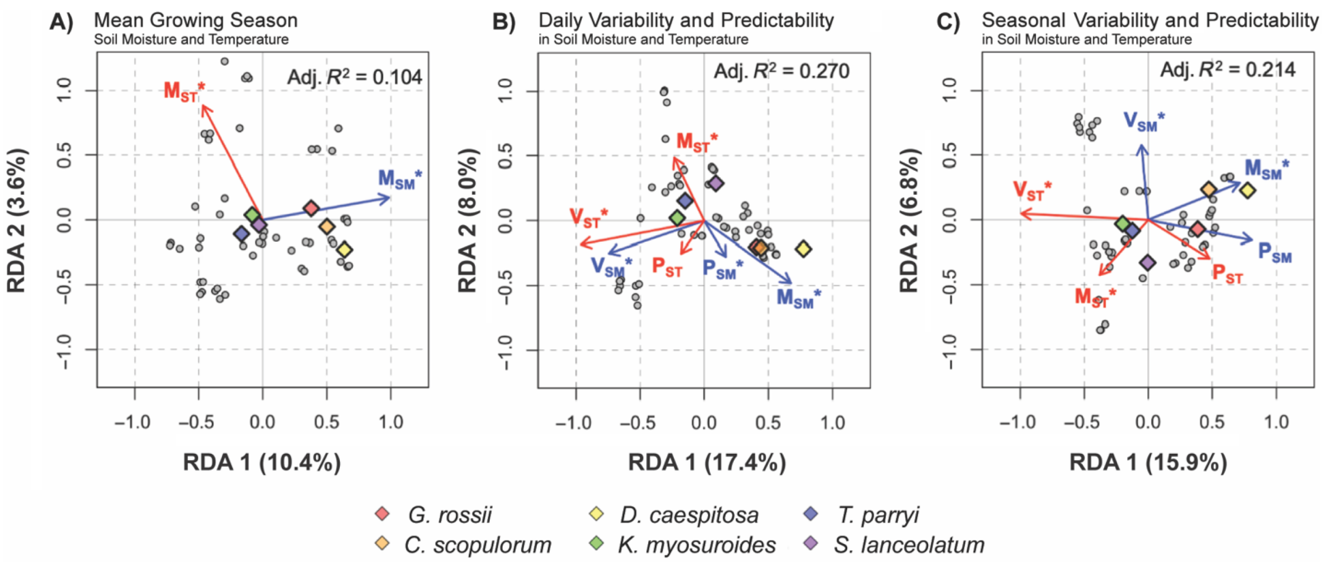

FIGURE 2 Effects of soil moisture and soil temperature on community structure at Niwot Ridge. Each panel shows the results of a redundancy analysis (RDA) evaluating the effects of (A) mean soil moisture (M_{SM}) and mean soil temperature (M_{ST}), (B) M_{SM}, M_{ST}, and daily soil moisture and temperature variability (V_{SM}, V_{ST}), predictability (P_{SM}, P_{ST}), and (C) seasonal M_{SM}, M_{ST}, V_{SM}, V_{ST}, P_{SM}, and P_{ST} on community structure. In all panels, an * indicates $p < 0.05$ for the indicated term in the RDA. Gray circles represent the community composition measured at each node ieach year of the study (2018, 2019, 2020, and 2021), placed along the x and y axes to reflect their relative positions along the two multivariate axes of community composition that explain the most variation in the data set. The arrows represent the environmental predictor variables included in each model. Colored diamonds indicate the positions of the six highlighted plant species within community space and relative to the soil moisture and temperature axes.

Mean soil temperature (3.8%, $p = 0.01$) and seasonal variability in soil temperature (3.8%, $p = 0.016$) again explained similar amounts of variation in community composition. Finally, seasonal predictability in soil moisture and temperature were not important predictors of community composition, explaining only 2.0% ($p = 0.231$) and 1.5% ($p = 0.501$) of variation in plant community structure, respectively.

Variability and predictability as predictors of species distributions and abundances

We detected few significant relationships between overall species occurrences and abundances and variation in soil moisture and temperature in the Sensor Network Array vegetation plots. On average, species occurrences showed a tendency to decline with increasing mean soil moisture (odds ratio < 1, $p = 0.02$) and increase with variability in soil temperature (odds ratio > 1, $p = 0.001$) (Appendix S1: Table S3). No other environmental predictors explained significant levels of variation in overall species occurrences and abundances (Appendix S1: Tables S3–S6), nor did variation among years, with marginal R^2 values (which quantifies the amount of variation explained by the fixed effects alone) of 0 or near 0 in all models. In contrast, there was significant support for including species-specific responses to environmental predictors in the model (i.e., random slopes for species) for all predictor variables except those evaluating species abundances as a function of daily predictability and seasonal variability in soil temperature (Table 1). The explanatory power of the random effect structure in models where random slopes were supported had conditional R^2 values ranging from 52% to 66% (Table 1).

We used the CIs around conditional median estimates for the random slopes in these models to determine whether and how often the probability of occurrence of individual species was influenced by the mean, variability, or predictability of the environmental variables. We found that 66% of the 87 species in our data set (Figure 3A) had at least one significant relationship (i.e., the CIs did not overlap zero) with the overall mean, daily variability, or daily predictability in soil moisture or temperature, while 43% had at least one significant relationship in the corresponding analyses with seasonal timescales (Figure 3B). In both cases, more than half of the significant relationships were in association with metrics of variability or predictability, with fewer total found with the overall mean environmental conditions (Figure 3A,B). The occurrence patterns of many species, including the six species we examined individually, were

TABLE 1 Conditional R^2 values[a] for models of species occurrences and abundances and each of six tested predictors.

	M_{SM}	M_{ST}	V_{SM}	V_{ST}	P_{SM}	P_{ST}
Occurrence						
Daily	**0.56**[b] (0.44)	**0.50** (0.44)	**0.59** (0.44)	**0.61**[c] (0.44)	**0.45** (0.44)	**0.48** (0.44)
Seasonal	**0.56**[b] (0.44)	**0.50** (0.44)	**0.58**[b] (0.44)	**0.46** (0.44)	**0.52** (0.44)	**0.48** (0.44)
Abundance						
Daily	**0.59** (0.54)	**0.57** (0.54)	**0.57** (0.54)	**0.60** (0.54)	**0.55** (0.54)	**NS**
Seasonal	**0.59** (0.54)	**0.57** (0.54)	**0.59** (0.54)	**NS**	**0.57** (0.54)	**0.55** (0.54)

Abbreviations: M, mean; P, predictability; SM, soil moisture; ST, soil temperature; V, variability.

[a]Conditional R^2 values for generalized linear mixed models including random intercepts and slopes for species (bolded terms) and the corresponding model without random slopes for species (unbolded terms, in parentheses). NS is the model with a random effect for species slopes was not supported over a model without random slopes ($p > 0.05$); in all other cases, the model with random slopes and intercepts explained significantly more variation than the intercept-only model ($p < 0.05$).

[b]Marginal $R^2 = 0.02$.

[c]Marginal $R^2 = 0.05$. All other marginal R^2 values were estimated to be less than 0.01 or zero.

related to some, but not all, of the environmental predictors (Figure 4A,B). For example, the probability of occurrence of *C. scopulorum* and *D. cespitosa* increased with mean soil moisture, declined with soil moisture variability, and had no relationship with soil moisture predictability (Figure 4A). Overall, daily and seasonal variability in soil moisture was particularly important in differentiating the occurrence patterns of plants in our data set (Table 1, Figure 3; Appendix S1: Tables S3 and S4).

In general, patterns of species' abundances were less sensitive to environmental variability and predictability than their occurrences, with only 30% (Figure 3C) and 24% (Figure 3D) of the species, respectively, having random slope estimates (medians ± 95% CIs) that did not overlap 0. We saw no overall directional relationships between total species abundance and any of the environmental predictors (Appendix S1: Tables S5 and S6). Instead, we observed a wide distribution of responses across species for each predictor, indicated by the range of random slope estimates, as well as varied responses across predictors within a species. For example, *G. rossii*'s abundance decreased with increasing variability in soil moisture but had the opposite relationship with predictability in soil moisture (Figure 4C,D) at both daily and seasonal timescales. We did not find support for the specified random effect structure for predictability in soil temperature at daily timescales or variability in soil temperature at seasonal timescales.

For many species, the effects of environmental variables on individual species' occurrence and abundance often differed across timescales, with the same environmental variable at seasonal and daily timescales showing contrasting effects on distribution patterns. For example, the probability of occurrence of *T. parryi*, *C. scopulorum*, and *D. cespitosa* (common moist meadow graminoids) declined with increasing daily variability in temperature (Figure 4A) but showed no sensitivity to temperature variability over the seasonal timescale (Figure 4B).

Full model summaries including random effect variance estimates are provided in Appendix S1: Tables S2–S5.

DISCUSSION

Incorporating estimates of variability and predictability in soil moisture and temperature improved our ability to predict spatial variation in community composition and relative to models that relied on time-averaged estimates of these variables alone. Species had varying relationships with temporal variability, with the strength and direction of the association (positive or negative) depending on the species, environmental variable, and the timescale over which variables fluctuated. Together, our results suggest that species vary widely in their relationships with temporal environmental variation, as we would expect if different patterns and rates of environmental fluctuations favor alternative growth and life history strategies. Collectively, these results indicate that the axes of temporal variability provide important opportunities for differentiation among alpine tundra plant species that shape fine-scale differences in community composition across heterogeneous alpine terrain.

Species-specific responses to variability and predictability

Species' affinities for specific patterns of temporal variability and predictability can drive distribution and abundance patterns within communities when those patterns vary across the landscape, but these associations are rarely quantified (Terradas et al., 2009). Previous studies have documented that spatial variation in mean

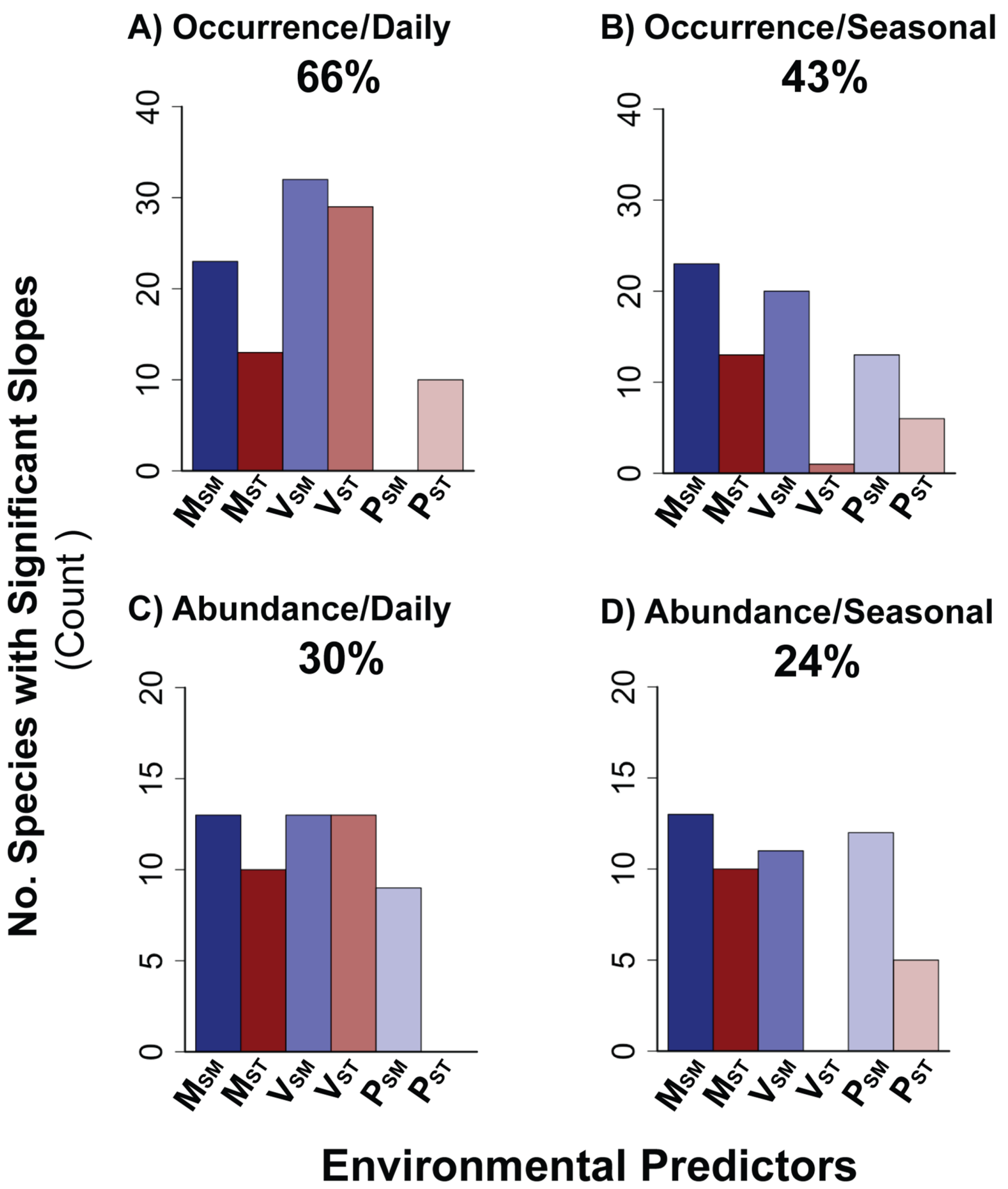

FIGURE 3 Total numbers of species with occurrence and abundance patterns that are significantly predicted by soil moisture and temperature variation at Niwot Ridge. (A) The number of species with nonzero slope estimates (i.e., with 95% CIs that do not overlap zero; see *Methods*) for the relationship between their occurrence (presence or absence) in a plot and daily variability and predictability in soil moisture and temperature. (B) The number of species with nonzero slope estimates for the relationship between their occurrence patterns and seasonal metrics of variability and predictability in soil moisture and temperature. (C) The number of species with nonzero relationships between their abundance and daily variability and predictability. There was no support for a random effect of species slopes for the model including predictability in soil temperature (P_{ST}). (D) The number of species with nonzero slopes for the relationships between their abundance and seasonal variability and predictability metrics. There was no support for a random effect of species slopes for the model including variability in soil temperature (V_{ST}). All panels also show the number of species with nonzero slope estimates in their occurrence (A, B) or abundance (C, D) and mean soil moisture and temperature. The percentages in each panel show the proportion of species with at least one nonzero slope (out of 87 total). Please see Figure 4 for the distributions of the random slopes for species' relationships with each environmental predictor, and Appendix S1: Tables S2–S5 for full model output. M, mean value (dark shading); P, predictability (light shading); SM, soil moisture (shades of red); ST, soil temperature (shades of blue); V, variability (medium shading).

temperature (Steinbauer et al., 2022) and soil moisture (Ehleringer & Miller, 1975; Foster et al., 2020) influence population growth rates and distribution patterns in alpine plant species (Abeli et al., 2012; Carlson et al., 2015; Kopp & Cleland, 2014). Our analysis of fine-scale spatial and temporal variation among nodes in

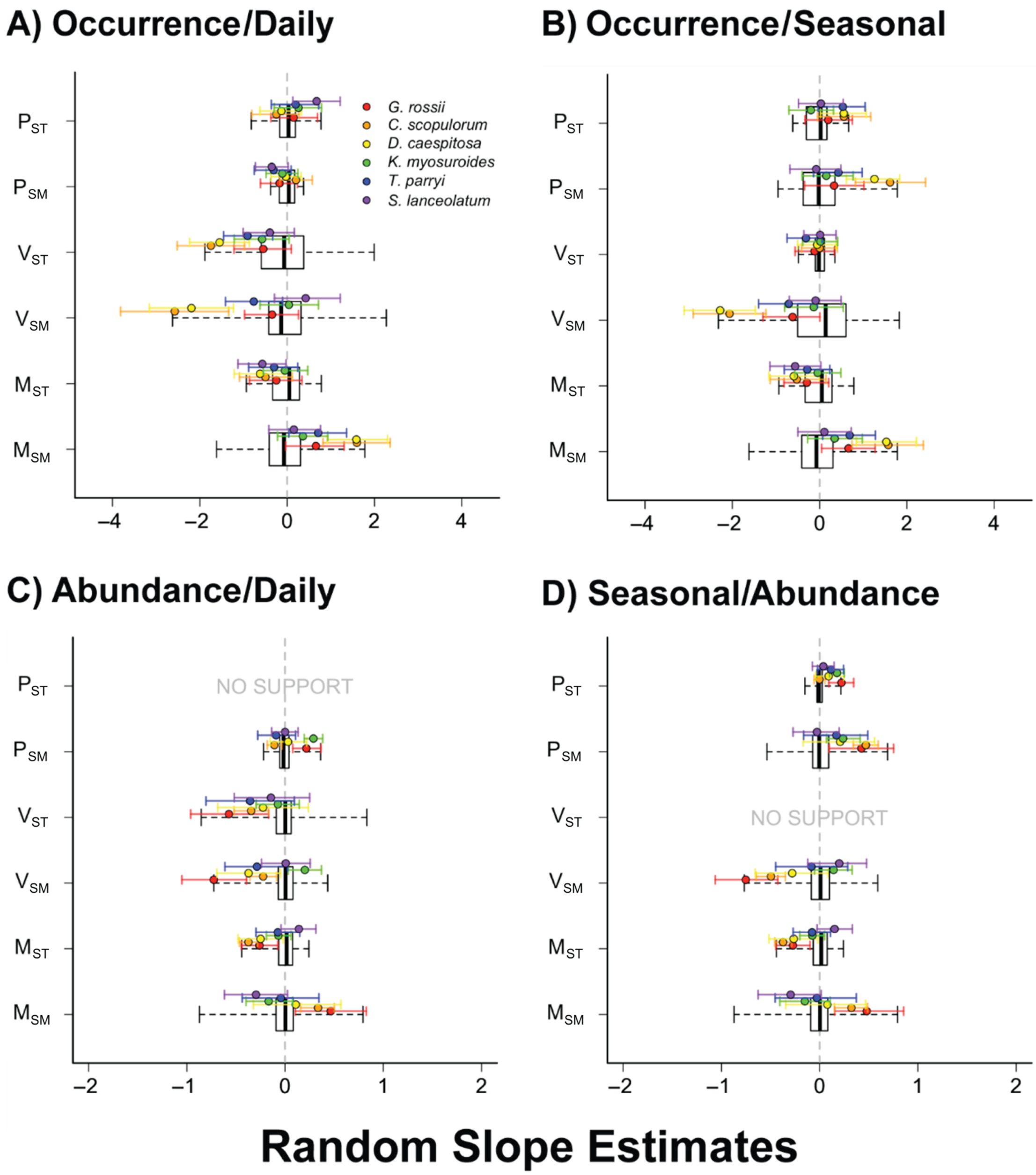

FIGURE 4 Variation among alpine plant species in their relationships with the annual mean, daily and seasonal variability, and daily and seasonal predictability in soil moisture and temperature. Panels (A) and (B) show the estimated slopes of relationships between species' occurrences and the mean, variability, and predictability of soil moisture and temperature measured over (A) daily and (B) seasonal timescales in the alpine vegetation at the Niwot Ridge Long-Term Ecological Research site. Panels (C) and (D) illustrate the estimated slopes of the relationships between species abundances and the mean, variability, and predictability of soil moisture and temperature measured over (C) daily and (D) seasonal timescales. Each boxplot shows the range of random slopes generated in a model with a singular predictor variable (e.g., mean soil temperature). Colored dots correspond to the six highlighted species that are common in the alpine plant community at Niwot Ridge (see *Methods*). The vertical line aligned with "0" on the *x*-axis represents no relationship between the predictor variable and species occurrence or abundance; boxplots to the left have a negative relationship between the predictor and response, while plots to the right indicate a positive relationship. No values were generated for relationships between species' abundances and the predictability of soil temperature (P_{ST}) at the daily scale or variability in soil temperature (P_{ST}) at the seasonal scale because there was no statistical support for including random slopes in those models (see Table 1; Appendix S1: Tables S4 and S5). Error bars show 95% CIs for each random slope estimate. M, means; P, predictability; SM, soil moisture; ST, soil temperature; V, variability.

the Sensor Network Array also detected relationships between plant community composition and mean soil moisture and temperature, reinforcing the importance of overall wet-dry and cold-hot gradients in shaping plant associations at Niwot Ridge. However, we further found that variability and predictability in soil moisture and temperature explained additional variation that the time-averaged variables alone did not capture (Table 1, Figures 3 and 4; Appendix S1: Tables S3–S6). In our analysis of six focal species, *C. scopulorum* and *D. cespitosa*—both wet meadow species—were most likely to occur in locations where soil moisture was high, consistent (low daily and seasonal variability), and predictable across the season (Figure 4A,B), perhaps reflecting mechanisms to track slowly drying conditions through adaptive phenotypic plasticity (Gill et al., 2022; March-Salas et al., 2022). The abundance of *K. myosuroides*—a dry meadow species—was particularly sensitive to soil moisture variability and predictability at daily timescales (Figure 4C), potentially reflecting the importance of intermittent rain events in driving soil moisture patterns in the dry meadow habitat. The widespread succulent *S. lanceolatum* was most likely to occur where daily soil moisture variability was high and relatively unpredictable (Figure 4A) and, in the plots it occupied, increased in abundance with increasingly warm and dry conditions (Figure 4C,D), suggesting that the relatively conservative growth strategy of this species might provide an advantage in relatively exposed habitats that rely on summer precipitation for moisture rather than snowmelt (Koshkin et al., 2021; Nevoux et al., 2010).

Our analyses of individual species' relationships with temporal variability and predictability were limited to taxa that were relatively abundant in our data set, and thus even the large variation we observed among them may represent a biased subset of what exists in this community. The vegetation and environmental monitoring project of the Sensor Network Array is a long-term data set for the Niwot LTER that will eventually provide opportunities to evaluate how species representing different functional groups, phylogenetic associations, and forms of rarity associate with axes of temporal variability, including inter-annual variation in conditions such as the timing of snowmelt and total length of the growing season. Longer time series will make it possible to include multiple axes of temporal variability into the same predictive models, tease apart the correlations among predictor variables, and test whether there are trade-offs among different axes of variability. It will also become possible to directly compare different measures of variability and predictability (e.g., CV vs. variance, autocorrelation within variables vs. correlations between different variables) and quantify how those metrics themselves change through time. Despite the large amount of time, effort, and expense invested in the data set presented here, we were still relatively data-sparse in the number of independent replicates we had available for this first analysis ($N = 13$ nodes sampled in four consecutive years), limiting our ability to dissect the relationships within and among axes of temporal variability that likely interact to shape plant community composition at Niwot Ridge (Appendix S1: Figures S1 and S2). For example, daily variability in soil moisture and soil temperature are correlated with one another, and both are negatively correlated with mean overall (time-averaged) soil moisture (Appendix S1: Figure S1), reflecting the dominant role of snowmelt in shaping moisture and temperature variation in space and time in the alpine. Only longer-term data collection, ideally coupled with manipulative experiments, can tease apart which (if any) of these axes and other environmental axes are the most important drivers of individual species distribution patterns in the alpine.

Life history theory predicts that the growth and reproductive strategies that are favored in an environment hinge heavily on the rate and pattern of environmental change relative to the rate at which organisms can respond through phenotypic plasticity (Botero et al., 2015; Orzack, 1985; Tuljapurkar, 1989). Species can only successfully respond to environmental changes through plasticity if they can sense shifting environments and then initiate physiological changes on timescales commensurate with the environmental shifts (Bernhardt et al., 2020; Terradas et al., 2009). At Niwot Ridge, we saw a striking difference between the extent to which daily and seasonal fluctuations in soil temperature predict the distributions and abundances of alpine plants, with daily variability in soil temperature explaining a large amount of the total variation in both response variables (Table 1) and for more species (Figure 3). Relatively rapid fluctuations can be impossible for organisms to track through phenotypic plasticity, favoring more conservative, slow life history strategies that allow persistence through periods of stress or resource limitation while limiting their ability to capitalize on periods of benign, resource-rich conditions. In alpine environments, diurnal fluctuations in temperature can provide information about a seed's location in the soil column and the extent of snow cover, with variability itself being a germination or dormancy cue in species that are adapted to seasonally snow-covered habitats (Fernández-Pascual et al., 2021). Studies have documented both interspecific (Fernández-Pascual et al., 2021) and intraspecific (Satyanti et al., 2019) variation in how temperature fluctuations influence alpine seed germination rates, suggesting that species responses to rapid fluctuations in soil temperature is an important axis of differentiation in this plant community.

Slower oscillations in environmental conditions generate temporal autocorrelation over timescales that are expected to favor adaptive phenotypic plasticity, as the conditions that occur at one time point can be used to predict those at some point in the future (Botero et al., 2015; Scheiner & Holt, 2012). That is, for the same magnitude of variability, slower changes and higher predictability should favor plasticity over fixed conservative and bet-hedging strategies. Seasonal patterns of soil moisture in the alpine can reflect topographic variation in the extent to which moisture is controlled by snowmelt (a relatively predictable water source) versus precipitation (an unpredictable source) over the growing season. We found that the seasonal predictability of soil moisture was more strongly associated with species' occurrence patterns than daily predictability (Table 1, Figure 3A,B), consistent with the expectation that alpine plants have differentiated in their associations with snowmelt versus precipitation as their primary source of moisture during the growing season.

Community responses to variability and predictability

Species-specific responses to temporal fluctuations in the environment are expected to play a critical role in driving patterns of coexistence and exclusion (Adler et al., 2010; Chesson, 1994, 2000) and community responses to future environmental change (Botero et al., 2015). Several different ecological mechanisms may explain how and why environmental variability and predictability influence plant community structure in alpine systems. For example, species' varied responses to different environment variables at multiple timescales (Figure 4) suggest that species may have evolved different strategies for managing temporal variation, a form of niche partitioning (Gavini et al., 2019; Morente-López et al., 2022; Terradas et al., 2009). Furthermore, species-specific responses to temporal variation could change the relative fitness of species within communities as soil moisture or temperature fluctuates (Danby & Hik, 2007). For example, even if two species exhibit the same preference for low variability in soil moisture (e.g., *D. cespitosa* and *C. scopulorum* in our study), one might have a relative fitness advantage at intermediate levels of soil moisture while the other has a slight advantage at higher and lower moisture levels. Variation in species' responses to temporal changes in the environment can generate compensatory dynamics, allowing aggregate community properties (such as total biomass) to remain constant while the abundances of individual species fluctuate through time (Doak et al., 1998; Schindler et al., 2015). Finally, species with opposite responses to the same variables can coexist if their abundances increase and decrease with differences in the timing of favorable conditions (e.g., wet and dry seasons) (Gonzalez & Loreau, 2009; Shoemaker et al., 2022). Future work will disentangle the relative importance of these mechanisms in driving the patterns we documented here using manipulative experiments or modeling approaches.

Conclusions and future work

We found that alpine plant community composition and the distributions of individual species are associated with variability and predictability in soil moisture and temperature across a heterogeneous landscape. While these measures of temporal variability improved our ability to predict plant population and community patterns, a large amount of variation in these patterns remains unexplained. It is likely that we could further improve the predictive power of our models by quantifying variability and predictability along other important environmental axes, many of which may occur over timescales that are not captured in the 4 years of our study. For example, the timing of snowmelt is an event that occurs only once/year, but varies substantially across the landscape and can be associated with plant community structure in ways beyond its impacts on soil moisture and temperature (Litaor et al., 2008). Finally, very little is known about the scale of dispersal in alpine plants, and it is possible that our 4-year data set did not provide enough time to adequately capture recruitment and extinction dynamics in these long-lived, perennial communities. Again, the longer time series that will develop with additional years of sampling in the Sensor Network Array will provide future opportunities to explore how dispersal and recruitment contribute to plant responses to temporal fluctuations at Niwot Ridge.

Our results indicate that patterns of temporal variability are critical components of niche space that may be as important, if not more so, than average conditions in explaining species' distribution patterns in complex environments. These axes are becoming increasingly important to understand as environments become more variable and unpredictable due to human impacts. Finally, the outcomes of this study underscore the immense value of long-term data sets that collect ecologically relevant environmental data at temporal resolutions that can be partitioned into different components (e.g., variability and predictability) and different timescales. Such data sets are essential to fully explore the diverse relationships between temporal niche axes, life history strategies, and species interactions that ultimately determine how communities respond to environmental change.

AUTHOR CONTRIBUTIONS

William J. Reed and Nancy C. Emery conceived the study. William J. Reed, Nancy C. Emery, William D. Bowman, and Niwot Ridge Long-Term Ecological Research staff and assistants collected the data. William J. Reed led the data analysis and interpretation with input from all authors. Aaron J. Westmoreland corroborated the analysis and finalized the R scripts. William J. Reed and Nancy C. Emery wrote the manuscript. All authors reviewed and provided feedback on drafts of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available in the Environmental Data Initiative's EDI Data Portal in the following data releases: Morse and Niwot Ridge (2022) at https://doi.org/10.6073/pasta/598894834ea3bae61d7550c30da06565; Reed et al. (2022) at https://doi.org/10.6073/pasta/dde8eed69de73b9c7947c778f15920ed. Code (w-reed, 2024) is available in Zenodo at https://doi.org/10.5281/zenodo.13629151.

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SUPPORTING INFORMATION

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

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