

Beyond arctic and alpine: the influence of winter climate on temperate ecosystems

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Abstract. Winter climate is expected to change under future climate scenarios, yet the majority of winter ecology research is focused in cold-climate ecosystems. In many temperate systems, it is unclear how winter climate relates to biotic responses during the growing season. The objective of this study was to examine how winter weather relates to plant and animal communities in a variety of terrestrial ecosystems ranging from warm deserts to alpine tundra. Specifically, we examined the association between winter weather and plant phenology, plant species richness, consumer abundance, and consumer richness in 11 terrestrial ecosystems associated with the U.S. Long-Term Ecological Research (LTER) Network. To varying degrees, winter precipitation and temperature were correlated with all biotic response variables. Bud break was tightly aligned with end of winter temperatures. For half the sites, winter weather was a better predictor of plant species richness than growing season weather. Warmer winters were correlated with lower consumer abundances in both temperate and alpine systems. Our findings suggest winter weather may have a strong influence on biotic activity during the growing season and should be considered in future studies investigating the effects of climate change on both alpine and temperate systems.

Key words: critical climate periods; ecosystem stability; global change; temperate ecosystem; U.S. LTER Network; winter.

INTRODUCTION

Winter seasons are present in many non-tropical biomes. While climate change is expected to be rapid and multifarious in most seasons and places (Serreze 2010, IPCC 2013), ecological research in temperate systems has mainly focused on either the implications of climate change during the growing season, or changes in annual averages of climate variables (e.g. mean annual precipitation). The contemporary view of climate change effects on biotic communities remains incomplete, as we do not understand the potential role of winter in year-round ecosystem functioning. Biotic responses to climate can exhibit seasonal lag effects

(Sala et al. 2012) and winter climate may strongly influence growing season activity (Haei et al. 2013, Mori et al. 2014). Although evidence for the importance of winter vs. summer climate on ecological processes is recently increasing (e.g. Haei et al. 2013, Mori et al. 2014, Schuerings et al. 2014), current research remains seasonally biased and largely neglects the influence of winter climate on ecological processes (Campbell et al. 2005, Kreyling 2010). This knowledge gap limits projections of ecological response to future climate scenarios, as many climate circulation models indicate equal or higher rates of climate change during winter than during the growing season (Plummer et al. 2006).

The majority of winter ecology research has focused in regions where winter forms a prominent season, such as arctic and tundra ecosystems (Inouye 2008, Wipf et al. 2009, Wipf and Rixen 2010) and to a lesser extent, northern temperate and boreal forests

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(Campbell et al. 2005, Kreyling 2010, Groffman et al. 2012). In arctic and boreal regions, winter climate plays a substantial role in nutrient (Wipf and Rixen 2010), carbon (Haei et al. 2013), and water cycling (Lapp et al. 2005), plant community composition (Walker et al. 1993, Inouye 2008, Wipf et al. 2009, Rammig et al. 2010, Bokhorst et al. 2011), and large consumer performance (Post et al. 2009). The question remains, however, as to whether or not similar relationships exist in many temperate and semiarid systems. Winter still institutes a well-defined dormant season in temperate and semiarid systems and may affect resource availability during the growing season (e.g., Germino and Reinhardt 2014). On the other hand, temperate and semiarid systems may not be as limited by growing season length, and higher rates of evapotranspiration during the growing season could supersede lag effects from the winter. Clearly a broader, more comprehensive understanding of ecosystem responses to winter climate is needed to develop a better mechanistic understanding of ecological processes in response to winter.

Perhaps the most direct ecological effect of winter weather is through the interaction of temperature and metabolic rates. As such, our current understanding of how changing winter climate influences temperate biota is heavily focused on studies of phenology (Cleland et al. 2007, Inouye 2008, Ibáñez et al. 2010, Cook et al. 2012, Augspurger 2013). In general, warmer temperatures lead to earlier bud break of plants (Hülber et al. 2010, Smith et al. 2012), with species that leaf out early in the spring being more sensitive to changing temperature. The timing of spring warming can also affect when insects emerge or animals come out of hibernation (Inouye et al. 2000). With our current understanding, it is difficult to scale up these direct impacts of winter weather to higher levels of biological organization, such as species abundance and diversity. However, assessing links to higher biological organization is critical because diversity is important for maintaining multi-functionality and resilience in ecosystems (Carpenter et al. 2012, Maestre et al. 2012).

To start, shifts in plant phenology can trigger a cascade of effects through higher levels of biological organization (i.e. populations, communities, and ecosystems; Smith et al. 2009). Longer time-scale effects of changing phenology may alter relationships between pollinator and host emergence, can result in trophic mismatch between producers and consumers, and may shift migratory patterns of birds and animals (Singer et al. 2013). Increased winter temperatures can also lengthen the growing season, allowing species with different temporal niches to coexist (Adler and Levine 2007), thus increasing diversity. Conversely, an earlier end to winter may promote the invasion of exotic species adapted to growing during the fringes of growing seasons (Bradley et al. 2010). Different species' phenological responses to climate change could alter competition for resources, and ultimately species composition or richness.

Winter weather may further affect species diversity and abundance by altering the overall availability of resources, not just their temporal distribution. For example, more winter precipitation may increase soil moisture and thereby increase productivity in water-limited ecosystems (Robertson et al. 2009, Germino and Reinhardt 2014, Li et al. 2015). On the other hand, earlier onset of the growing season may negatively impact water-sensitive species. Altered winter precipitation can also trigger state changes in plant communities, leading to shifts in consumer communities (Brown et al. 1997). In summary, the effects of winter weather on species diversity and abundance are difficult to predict because multiple direct, indirect, and interactive effects likely occur at once. Yet with so many potential mechanisms at play, we predict that the magnitude of ecological responses to winter weather could be similar in temperate and semiarid ecosystems when compared to arctic and alpine ecosystems.

Despite a relatively strong understanding of the importance of winter conditions in cold-climate ecosystems, few studies have sought to quantify relationships between winter weather and growing season dynamics in or across temperate systems. The objective of this study is to assess the relationships between winter precipitation and temperature and growing season plant phenology, plant species richness, consumer abundance, and consumer richness across a range of ecosystems represented in the U.S. Long-Term Ecological Research (LTER) Network. Specific research questions included (1) How strong is the association between temperate plant and animal communities and winter weather relative to other seasons? and (2) Do temperate and arctic/alpine/boreal communities exhibit similar associations with winter weather? To our knowledge, this is the first assessment of the importance of winter weather across a variety of ecosystems and will hopefully serve as a guide to focus future experimental and mechanistic investigations.

METHODS

We compared daily precipitation and temperature to annual ecological response variables to determine what period of the year had the strongest correlation with each response variable. Our approach utilized long-term data from the U.S. LTER Network, a nationwide network of sites that represent key ecosystem types in North America, with long-term data sets on climate, phenology, vegetation, and consumers (Table 1, Fig. 1, Appendix S1: Table S1).

Defining "winter"

We defined the timing and length of winter based on NOAA National Climatic Data Center (NCDC) freeze/frost probabilities for each site. The NCDC utilizes daily climate data from the past ~40 years to determine the 10%, 50%, and 90% probabilities of when the first

TABLE 1. Characteristics of each site.

Site		Ecosystem	Latitude (°N), Longitude (°W)	Elevation (m)	MAT (°C)	MAP (mm)	ANPP (g C/m ²)
Andrews	AND	coniferous forest	44.21, 122.26	1020	9.1 ± 6.2	2242 ± 4	500
Bonanza Creek	BNZ	taiga	64.86, 147.85	365	−1.1 ± 11.6	560 ± 0.2	300
Cedar Creek	CDR	tallgrass prairie	45.40, 93.20	282	6.7 ± 11.4	779 ± 1	189
Hubbard Brook	HBR	deciduous forest	43.94, 71.75	590	5.8 ± 9.4	1357 ± 0.3	705
Harvard Forest	HFR	deciduous forest	42.53, 72.19	330	7.3 ± 9.2	1105 ± 0.3	745
Jornada Basin	JRN	desert	32.62, 106.74	1188	17.6 ± 7.9	276 ± 0.5	122
Kellogg Biological Station	KBS	successional field (untilled)	42.40, 85.40	288	9.1 ± 9.2	891 ± 1	431
Konza Prairie	KNZ	tallgrass prairie	39.09, 96.58	382	12.6 ± 9.6	815 ± 1	469
Niwot Ridge	NWT	alpine tundra	39.99, 105.38	3528	−2.2 ± 7.5	1994 ± 3	209
Sevilleta	SEV	desert grassland	34.35, 106.88	1478	14.3 ± 8.3	230 ± 0.4	87
Shortgrass Steppe	SGS	shortgrass steppe	40.83, 104.72	1650	9.6 ± 8.4	363 ± 1	102

Notes: MAT, historic annual average daily temperature; MAP, historic annual average daily precipitation; ANPP, annual net primary production. Values are means ± SD. Data obtained from LTER website <http://www.lternet.edu/site-characteristics>.

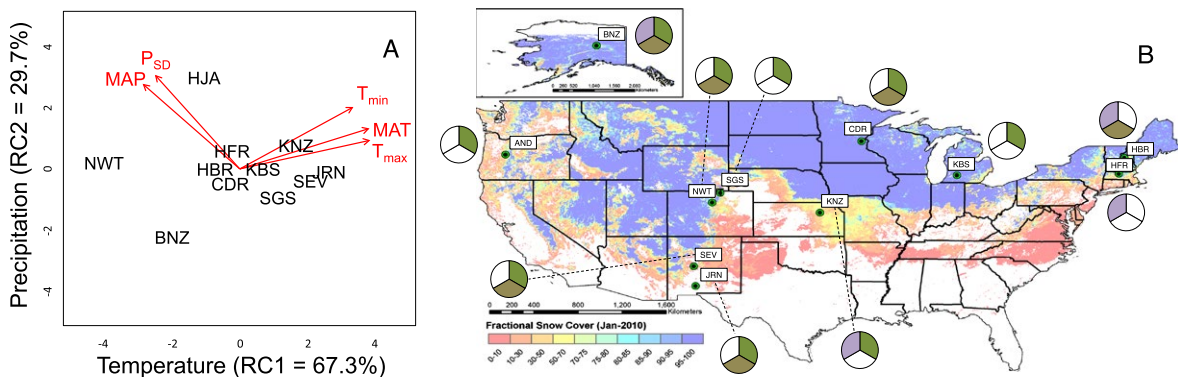


FIG. 1. (A) Sites arranged on principle components analysis (PCA) of daily climate variables indicated as vectors. Sites are identified in Table 1. MAP, historic annual average daily precipitation; P_{SD}, standard deviation of daily precipitation values across years; T_{min}, minimum air temperature; MAT, historic annual average daily temperature; T_{max}, maximum air temperature. (B) Site locations on a map of mean January snow cover. Pie charts associated with each site indicate which response variables were analyzed at each site: phenology, purple, upper left; plant species richness, green, upper right; consumer abundance or richness, brown, lower center.

and last frost of the year will occur. For our analysis, we selected the dates with a 90% probability of freeze (0°C) as the beginning and end of winter. In other words, there was a 90% chance of getting the first freeze before our start date and a 90% chance the last freeze event of the year occurring after our end date for winter (e.g. a 90% chance that the last freeze had not yet occurred). Compared to the 10% and 50% percentiles, the 90% probability resulted in the shortest winter season and was the most conservative measure of winter based on NCDC data. Data from the closest NOAA station to each site was used to calculate site-specific winter length and timing (Table 2).

Site and data selection

Sites represented a variety of terrestrial ecosystems in the temperate zone with different winter conditions

(Table 2), including hardwood forests (HBR, HFR), coniferous forest (AND), temperate grasslands (CDR, KBS, KNZ), and desert grasslands (JRN, SEV; Table 1; Fig. 1). Along with references to literature (e.g. Walker et al. 1993, Inouye 2008, Wipf et al. 2009, Rammig et al. 2010, Bokhorst et al. 2011), one alpine tundra site (NWT) and one boreal forest site (BNZ) were included for comparison between cold-dominated and warmer temperate ecosystems. We chose sites with long enough data sets (annual response variables with >7 yr, most data sets >10 yr) for at least one response variable (Fig. 1) and long-term daily weather measures (precipitation, air temperature). Weather among the sites was compared using a principal component analysis (PCA) of multiple variables for precipitation (historic annual average daily precipitation, MAP; standard deviation of daily precipitation values across years, P_{SD}) and temperature (historic annual average daily

TABLE 2. Winter conditions for each site.

Site	Winter			Winter air temperature (°C)	Winter precipitation (mm)	Annual precipitation (%)	NOAA NCDC data location
	Start	End	Days				
AND	23 Oct	10 Apr	170	3.4 ± 1.7	1711 ± 2	76	Cascadia, Oregon
BNZ	21 Sep	7 May	229	-9.8 ± 6.5	343 ± 0.3	61	Fairbanks, Alaska
CDR	6 Oct	25 Apr	202	-2.3 ± 6.9	250 ± 0.5	32	Cambridge Hospital, Minnesota
HBR	30 Sep	9 May	222	-0.8 ± 5.8	800 ± 0.4	59	Plymouth, New Hampshire
HFR	7 Oct	28 Apr	204	0.1 ± 5.2	591 ± 0.3	54	Tully Lake, Massachusetts
JRN	3 Nov	16 Apr	165	9.9 ± 3.4	71 ± 0.1	26	Jornada Basin, New Mexico
KBS	19 Oct	26 Apr	190	1.2 ± 4.6	367 ± 0.5	41	Battle Creek, Michigan
KNZ	29 Oct	5 Apr	159	2.9 ± 3.9	180 ± 0.5	22	Manhattan, Kansas
NWT	26 Sep	18 May	235	-7.1 ± 4.0	1671 ± 2	84	Evergreen, Colorado
SEV	30 Oct	12 Apr	165	6.2 ± 3.4	59 ± 0.1	26	Socorro, New Mexico
SGS	14 Oct	21 Apr	190	2.4 ± 3.5	83 ± 0.3	23	Greeley UNC, Colorado

Note: Values are mean $\pm$ SD.

temperature, MAT; maximum air temperature, $T_{\max}$; minimum air temperature, $T_{\min}$).

Our biotic variables included plant phenology, plant species richness, consumer richness, and consumer abundance. For plant phenology, we used the date of bud break. Long-term, detailed (daily or weekly) phenology records were more consistently available for woody species, whereas data from herbaceous species were sparse; therefore no herbaceous plants were included in phenology assessments. Bud break measurements slightly varied between sites and were associated with either the arrival of first full leaf (BNZ, HBR, HFR; Bailey 2013) or date of first flower (KNZ). Bud break is often associated with increasing temperature at the end of winter (Cook et al. 2012), therefore examining bud break provided a good test of the ecological relevance of our definition of winter. Plant species richness is an important metric of ecosystem structure, and most sites had long-term measures of plant species richness, making this a salient, consistent variable for comparison across the range of sites. Methods for measuring plant species richness varied between sites as approaches were geared towards capturing locally important components of biodiversity at each site but still allowed for mechanistic comparisons across sites. Plant species richness varied between sites, and mean ($\pm$ SE) number of species/1 m² ranged from 4 ± 1 in taiga (BNZ) to 31 ± 1 in tallgrass prairie (KNZ; Appendix S1: Table S1). However, direct comparisons of species richness across sites were not possible because plot sizes differed. Half the sites had long-term consumer data, but taxa varied between sites because focal consumers were chosen by local investigators. Rodent communities were assessed within desert grasslands (SEV) and alpine tundra (NWT). Lizard communities were measured in desert grasslands (JRN). Insects were evaluated at other sites, specifically populations of three caterpillar species in hardwood forest (HBR; Holmes 2013), grasshoppers from temperate grassland (CDR), and three beetle taxa in boreal forest

(BNZ; Appendix S1: Table S1). Similar to plant species richness, richness and abundance of consumers also varied between sites (Appendix S1: Table S1).

Data analysis

It has long been known that small periods of climate variability can have greater impacts on ecosystem function than annual climate variables would predict, and researchers have worked to identify these periods of time in a range of systems (sensu Smoliak 1986, Lauenroth and Sala 1992, Derner and Hart 2007). The term Critical Climate Period (CCP) was recently used (Craine et al. 2012) to describe the period(s) of the year when climate has the strongest correlation with a response variable of ecosystem structure and/or function. CCP analysis differs from previous techniques in that it does not rely on any a priori biases on when climate is most important, but instead looks for the correlations between a response variable and climate statistics calculated for a wide range of “climate periods” calculated across a temporal gradient (T. W. Ocheltree, N. Brunsell, J. Nippert, Z. Ratajczak et al., *unpublished manuscript*). For CCP analysis, climate statistics were calculated for all possible climate periods by varying the starting date and the size of the climate period (number of days), which includes all possible time window lengths and starting times throughout the year.

$$CP_{i,w} = f \sum_{i=1}^w x_i \quad (1)$$

where CP is the climate period, i is the starting day of the year (DOY; day 1 being the first day of the growing season year), w is the window size for each CP, and f is the function to be applied to the climate variable of interest (e.g. sum of precipitation). For our study, the starting date for climate periods spanned the entire growing season year. The length of the climate periods at any one starting date varied from 10 to 365 d (at 10 d

intervals), which resulted in 5780 climate periods for each year of data available. Rather than using calendar years, we used “growing season year,” which ran from the beginning of one winter to the next. For example, if winter began on DOY 258 (described in *Defining winter*), then the growing season year was calculated as DOY 258 of one year through DOY 257 of the next. Climate data from the year prior to each biotic measurement were used to include lag effects from the previous year (i.e. legacy effects) and to ensure that the particular climate window could have influenced the response variable.

To find the climate period(s) that explained the greatest variation in the response variable, a correlation matrix between every possible CP and the response variable was generated. All statistically significant CPs are reported and the CP with the strongest correlation (i.e. highest r^2 value) was selected as the critical CP (CCP). The CCP for the explanatory variable (precipitation or temperature) with the strongest correlation with the response variable was calculated first and the residuals from this regression were used to identify the CCP for the second explanatory variable. In many systems, precipitation had a greater correlation with response variables and was typically selected first before temperature CCPs.

The CCP approach requires long-term data to provide enough data to accurately depict the ecosystem through correlations between biotic response and climate and remove potential statistical bias from anomalous years. Even with long-term data sets, some statistical anomalies are likely when calculating so many different correlations. In order to prevent a single anomalous point from driving the regression statistics, a regression with a data point that leveraged the regression by $>3p/n$ was removed, where p was the number of parameters in the regression model and n was the number of years included in the regression. CPs driven by anomalous points were removed prior to assigning a CPP. This approach does not remove an entire year, or years, from the analyses, it only serves to flag specific CPs where a high r^2 is highly dependent on a single data point. Despite our efforts to avoid anomalous data with leverage analysis, some outliers may remain and lead to the assignment of random CPs throughout the year. However, if all the significant CPs tend to fall around the same time of year, it is a good indication that CPs reflect actual associations between the response variable and weather fluctuations during that time of the year rather than statistical anomalies. To locate problematic random CPs, we plotted all significant CPs for precipitation and temperature ($P < 0.01$) along with the CCP to visually inspect whether our approach was selecting random CPs throughout the year.

To determine if the CCP occurred during winter, we examined if the timing of the critical climate period aligned with our defined length of winter. Some winter CCPs fell completely within winter, while others occurred

both in winter and a neighboring season, typically spring. We used the nonparametric Mann-Whitney U test to determine if the CCPs that included winter had different correlation coefficients than non-winter CCPs. To test our assumptions against a null model we ran a randomized permutation test. For the permutation test, we randomly assigned all of our CCPs to two groups for each response variable, and then calculated to the 0.1%, 1%, and 5% quantiles from this population of P values. Finally, we compared our observed P values from the winter/non-winter analysis to the quantiles of the permutation test to determine if the difference between our winter and non-winter P -values were smaller than would be expected from randomly assigned groups. To be conservative, we only considered P values from the Mann-Whitney U test to be statistically significant if they were lower than the 0.1% quantile values of the permutation tests. All analysis was run using R version 2.15.2 (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Our sites covered wide ranges in temperature and precipitation, which was highlighted in the environmental PCA (Fig. 1A). The first two principle components accounted for a total of 97% of the climatic variation between sites (Fig. 1A). The first PC explained 67% of the variation among sites and primarily separated hot/dry sites from cold/wet sites. The second PC explained 30% of the variability and further separated wet sites with high interannual variability in precipitation from drier sites with less variable precipitation. Winter length also varied among sites, ranging from 159 d in the tallgrass prairie (KNZ) to 235 d in alpine tundra (NWT, Table 2). Mean winter air temperature ranged from -9.8°C in boreal forest (BNZ) to 9.9°C in desert grassland (JRN). The lowest winter precipitation occurred in desert grassland (59 mm; SEV) and highest in coniferous forest (1711 mm; AND). For all biotic responses, CCPs occurred significantly more in winter than by random chance. With the exception of the consumer species richness and temperature, all P values from Mann-Whitney U tests were less than the values of the 0.1% quantile of the null distribution (Table 3). However, specific importance of winter varied across response variables and sites.

Phenology was strongly correlated with winter weather for nearly all species examined within tallgrass prairie (KNZ), hardwood forest (HBR, HFR), and boreal forest (BNZ). Most phenology CCPs occurred during winter or the transition between winter and spring (Fig. 2). Bud break was more strongly correlated with temperature than with precipitation ($P < 0.001$); the partial r^2 values were 0.75 and 0.15 for temperature and precipitation, respectively. Warmer winter temperatures generally corresponded with earlier bud break, with the exception of the deciduous tree *Betula lenta*

TABLE 3. *P* values from Mann-Whitney *U* tests and 0.1% quantile values from permutation analysis.

Biotic response	Precipitation		Temperature	
	Mann-Whitney	0.1% quantile	Mann-Whitney	0.1% quantile
Phenology	<0.0001	0.0020	<0.0001	0.0010
Plant species richness	<0.0001	0.0020	<0.0001	0.0020
Consumer abundance	<0.0001	0.0030	<0.0001	0.0020
Consumer species richness	<0.0001	0.0005	0.0008	0.0007

Note: Values in boldface type are statistically significant ($P < 0.05$).

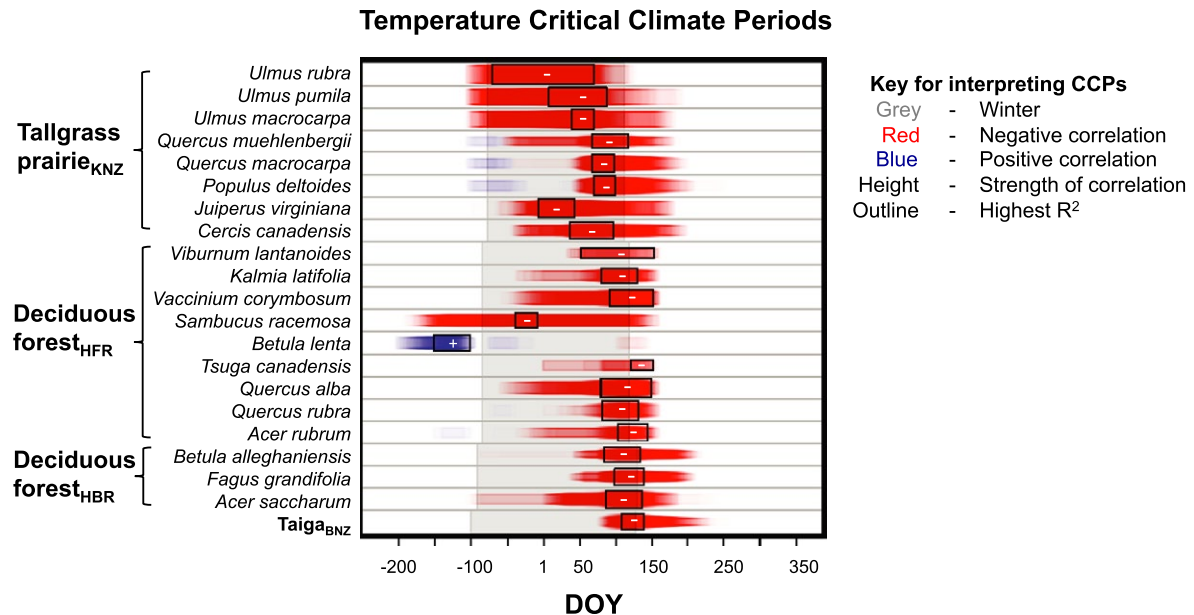


FIG. 2. Critical climate periods (CCPs) for the relation between temperature and phenology, indicated by color. Red indicates a negative correlation and blue indicates a positive correlation. The intensity of color indicates overlapping CPs. Height of colored bar represents correlation strength, with wide bars that fill the height of a row equal to an absolute value of 1 and narrow bars closer to 0. The time period with the highest r^2 for the correlations was designated as the critical CP (CCP) and is outlined in black. Gray shading indicates the timing of winter. Sites are arranged by length of winter, from shortest (top) to longest (bottom). DOY, day of year.

in hardwood forests (Fig. 2). Bud break for species at the warmest site (KNZ) had earlier CCPs for both temperature and precipitation than cooler sites.

The timing, duration, and direction of temperature and precipitation CCPs associated with plant species richness varied among sites (Fig. 3). The duration of the most predictive CCPs between weather and species richness ranged from 30 to 270 d. The direction of correlation between plant species richness and weather during the CCP also varied among ecosystems, and roughly half of the CCP correlations were negative and half were positive (Fig. 3). For both precipitation and temperature, half the sites had CCPs during winter, while the other half of sites had CCPs during another season. At many sites where CCPs occurred in other seasons, weaker correlations also occurred in winter. Overall, species richness was more strongly correlated to precipitation

(CCPs set at $\alpha = 0.05$) than temperature (CCPs set at $\alpha = 0.10$), because these relationships were weaker.

Less long-term data were available for consumer communities than producers, yet correlations between winter weather and animal communities were apparent. Consumer richness and abundance were correlated to winter weather to varying degrees. At all sites, CCPs occurred during winter for at least temperature or precipitation (Fig. 4). Specifically, winter precipitation was positively correlated with the richness of grasshoppers in temperate grassland (CDR), and negatively correlated with caterpillar richness in hardwood forest (HBR) and alpine rodent richness (NWT). Meanwhile, increased winter temperatures corresponded with decreased abundance of rodents in desert grassland (SEV) and alpine tundra (NWT), and caterpillars in hardwood forest (HBR) and beetles in boreal forest (BNZ; Fig. 4).

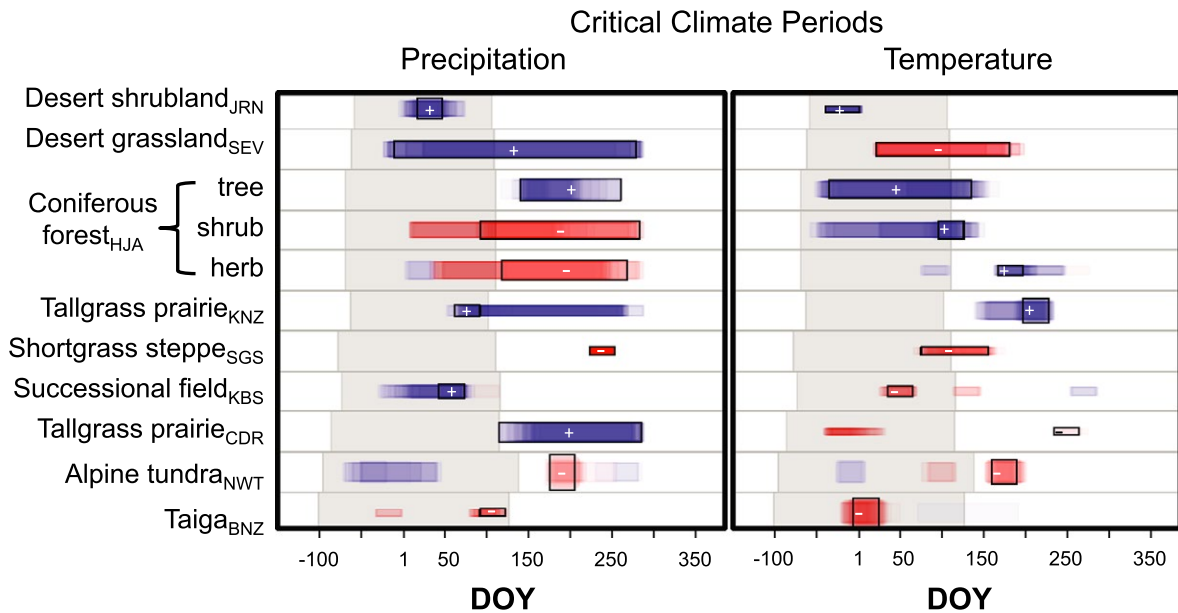


FIG. 3. CCPs for plant species richness with regard to precipitation and temperature. Sites are arranged by length of winter, indicated by gray shading, with shortest winters on the top and longer winters on the bottom. For details on CCP interpretation, see Fig. 2 caption.

DISCUSSION

Across a variety of ecosystems, both plant and animal communities had distinct associations with winter, separate from that of the growing season. In response to our first question examining the strength of the association between temperate plant and animal communities and winter weather relative to other seasons, the critical climate period for at least one biotic response variable (bud break, plant richness, consumer abundance and richness) occurred during winter for all ecosystems examined. Although significant, correlations between winter weather and biotic responses were variable among sites and biotic variables.

Plant phenology had the strongest correlations to winter temperature, particularly at the end of winter. The negative correlations between timing of bud break and end of winter temperature agree with the well-established relationship between warmer temperatures and earlier bud break (Cleland et al. 2007, Ibáñez et al. 2010, Cook et al. 2012, Pope et al. 2013). Phenology CCPs during the end of winter indicated that our definition of winter was able to accurately capture the end of winter when plants are responsive to warming temperatures. Only two of the 21 species studied here had CCPs outside the designated winter period, one of which (*Tsuga canadensis* (L.) Carr.) occurred a few days after the end of winter. Although temperature is generally considered the predominant driver of bud break (Cook et al. 2012), many plant phenology studies occur in temperate forests where soil moisture may not be limiting at the time of bud break. In drier systems, such as the Sonoran Desert,

plant phenology is more strongly linked to precipitation than to temperature (Crimmins et al. 2011). Therefore the influence of precipitation on phenology may be masked by stronger correlation with temperature and/or the bias of phenology studies in more mesic environments.

Associations between plant species richness and winter weather were variable among sites, with both positive, negative, and neutral associations. Yet, for half the sites, the critical climate period fell fully or partially in winter. Precipitation and temperature influence ecosystem structure and species richness at large spatial (Field et al. 2009) and temporal scales (De Boeck et al. 2011), and results from this study suggest that winter weather can significantly influence these interactions. Correlations between winter weather and richness were also likely related to diverse species-specific responses to precipitation regimes. For example, in many grasslands, rain may trigger high establishment of annual plants, and winter precipitation recharges groundwater reserves, the favored water source of many subdominant species (Nippert and Knapp 2007). In these cases, winter precipitation effectively increases the availability of rare species' niches, thus increasing species richness in years with greater winter precipitation. Drought may lower species richness due to losses of annual, ruderal, or rare species in a variety of ecosystems (Tilman and El Haddi 1992, Yurkonis and Meiners 2006, Fry et al. 2013, but see Adler and Levine 2007), or increase species richness if dominant plants suffer drought damage that allows ruderals to increase (Evans et al. 2011). Additionally, winter precipitation and temperature likely interact to shape plant

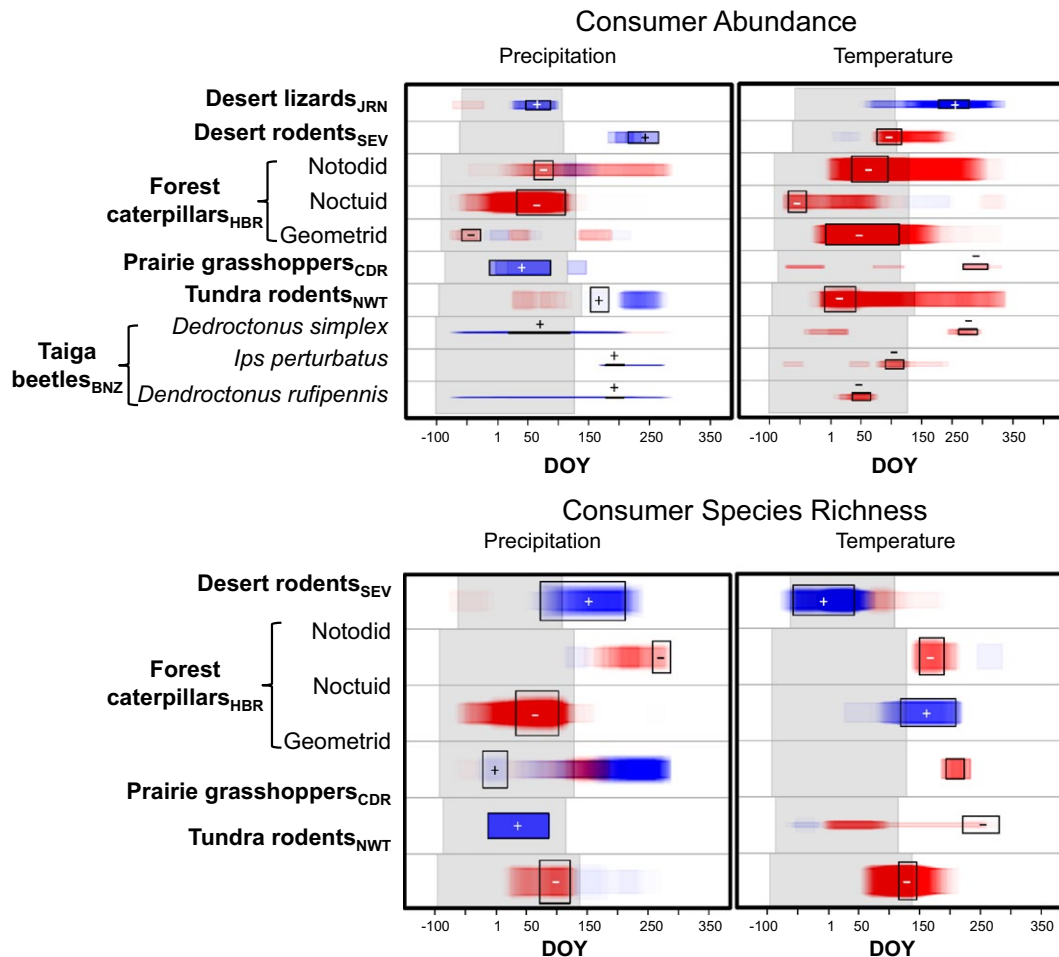


FIG. 4. CCPs for consumer species richness (top) and abundance (bottom). Sites are arranged by length of winter, indicated by gray shading, with shortest winters on the top and longer winters on the bottom. For details on CCP interpretation, see Fig. 2 caption. Further information about the consumer communities can be found in Appendix S1: Table S1. CCPs that are surrounded by other statistically significant CPs are more likely to reflect a biologically meaningful correlation between the CCP and response variable.

communities. Wetter winters correlated with lower species richness in boreal forest (BNZ) and shrub and herbaceous communities in northwestern coniferous forest (AND), both of which receive the majority of annual precipitation in the winter. Such complex dynamics might explain why associations between winter weather and plant species richness varied between sites in the present study. Future experimental work focused on changes in winter weather will increase our understanding of how plant species richness responds to climate variability.

Consumer abundance and richness were also correlated with winter precipitation and temperature to varying extents. Consumer abundance declined in nearly all communities under warmer conditions with the strongest climate periods occurring in winter. Above average winter temperatures may have an indirect negative effect on consumers via food or habitat resources (Brown et al. 1997). Depending on the plasticity of producers

and consumers, trophic mismatch can occur if warmer winters cause consumers to break hibernation before plant production begins (Inouye et al. 2000) or more likely, if producers cannot track earlier flushes of biomass brought on by shorter winters. Warmer winters could also affect metabolic rates. Insect performance and survival generally relate to temperature, particularly during winter, and vary greatly among species and habitats (Bale et al. 2002). Prolonged or intense snow cover and low temperatures may reduce winter food resources for rodents and reduce populations in the following season (Korslund and Steen 2006). Although prolonged cold can be beneficial. Colder winters in alpine systems are often associated with more snow cover, which provides better insulation from cold temperatures (Erb et al., 2011, Bhattacharyya et al. 2014). Our consumer data represent a diverse array of organisms and habitats (e.g., desert rodents, boreal forest beetles, hardwood forest caterpillar, prairie grasshoppers,

desert lizards, alpine tundra rodents), and perhaps are too diverse to draw a single conclusion. However, even with this limitation, consumer abundances were negatively correlated with winter temperature, suggesting some generality and potential declines in consumer populations with continued winter climate change.

Overall, winter weather was correlated with biotic responses across a variety of systems, and often this correlation was as strong or stronger than that of growing season weather and biotic responses (Figs. 2–4). The associations of plant species richness and consumer dynamics to winter climate were less consistent than those of phenology. This might be expected since plant phenology is often driven by temperature-sensitive physiological processes and frost damage avoidance (Arora et al. 2003). In contrast, plant and animal communities are shaped by the interactions of climate-related variables, (e.g., soil moisture, temperature, soil N, etc.) and other biotic and abiotic factors (e.g., competition, resource availability, site history, multiple species-specific responses, etc.). Thus, our ability to generalize the association between winter weather and biotic factors decreases as we move from population to community and ecosystem scale measurements.

Significant winter CCPs occurred for all response variables, yet the CCP analysis only provides a partial evaluation of the association between winter weather and biotic response. The process of averaging across a CCP and focusing on precipitation amount misses climate anomalies, such as ice storms or extreme cold events, which can alter community composition (Rhoads et al. 2002, Weeks et al. 2009), and decrease productivity (Ladwig 2014). Additionally, various factors of climate change can interact. Shorter, warmer winters may lead to earlier bud break, but increased climate variability could lead to more frequent damaging freeze events occurring after bud break (e.g., Bokhorst et al. 2008, Augspurger 2013). Therefore, our study provides a baseline association between winter climate and ecological communities but likely underestimates the influence of winter climate on growing season dynamics. To understand the impact of low-frequency extreme events or interactions between climate change factors we will need to continue on-going monitoring of these ecosystems.

In response to our second question, do temperate and polar communities exhibit similar associations with winter weather, we found that responses in boreal and alpine systems, cold-climate systems typical of much winter ecology research, were not good predictors for winter relations in temperate regions. One obvious contributor to these differences is the role snow, which is only common in half of our study sites. Although we were not able to include snowpack in our analysis because such data were unavailable for most temperate sites, the depth and duration of snowpack is known to be a particularly influential component of winter (Campbell et al. 2005) and may impact temperate sites

with more snow cover (i.e. SGS, CDR, KBS). Snow is an important insulator and as snow cover changes, temperature and water availability concurrently change, altering species assembly (Kreyling et al. 2012) and species richness (Loik et al. 2013). Increased snowpack could extend water availability later into the growing season, allowing plants to take up more nutrients during the summer. Alternatively, earlier snow melt from warmer spring temperatures can increase the mobility of nitrogen at a time when root uptake is low, resulting in increased losses of nitrogen through leaching and denitrification (Likens and Bormann 1995, Darrouzet-Nardi and Bowman 2011). Given the potential influence of snow on biotic processes across systems, more regular monitoring of snow pack depth and duration should be considered in long-term research sites.

A particularly interesting result from this study is that winter had such a strong correlation with biotic response variables, even though snow, one of the primary mechanisms invoked to explain impacts of winter on arctic/alpine ecosystems, is rare or absent from over half of our sites (Fig. 1). In fact, similar amounts of variability were explained by winter CCPs for boreal/alpine and temperate sites, indicating that winter was equally influential at sites with distinct climates. Given the potential importance of winter on community dynamics, it is critical to study the influence of winter in both temperate and alpine regions. The fact that winter could have such a strong influence on temperate sites, despite their near-lack of snow and ice, suggests that some winter effects in arctic and alpine systems might not be exclusively due to mechanisms related to frozen precipitation.

CONCLUSIONS

Winter climate should be considered a potentially important driver of contemporary and future ecosystem structure and function in regions that experience a cold season. In temperate systems, as in the arctic and alpine, both winter temperature and precipitation can influence growing season dynamics. However, the relationship between winter climate and ecological processes varies between ecosystems. In general, warmer temperatures led to earlier growing seasons with lower consumer abundance. To the best of our knowledge, this study provides the first assessment of the relation between winter climate and growing season variables across a range of taxa and ecosystems. Future studies investigating the response of growing season dynamics to climate change should also consider the influence of changes in winter climate.

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