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Threshold Changes in Winter Temperature and Precipitation Drive Threshold Responses Across Nine Global Climate Zones and Associated Biomes

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Abstract

Globally, winter temperatures are rising, and snowpack is shrinking or disappearing entirely. Despite previous research and published literature reviews, it remains unknown whether biomes across the globe will cross important thresholds in winter temperature and precipitation that will lead to significant ecological changes. Here, we combine the widely used Köppen–Geiger climate classification system with worst-case-scenario projected changes in global monthly temperature and precipitation to illustrate how multiple climatic zones across Earth may experience shifting winter conditions by the end of this century. We then examine how these shifts may affect ecosystems within corresponding biomes. Our analysis demonstrates potential widespread losses of extreme cold (<−20°C) in Arctic, boreal, and cool temperate regions. We also show the possible disappearance of freezing temperatures (<0°C) and large decreases in snowfall in warm temperate and dryland areas. We identify important and potentially irreversible ecological changes associated with crossing these winter climate thresholds.

1. INTRODUCTION

Winter has historically been considered a dormant period in ecosystems that experience below-freezing temperatures and seasonal snow cover (Campbell et al. 2005, Sanders-DeMott et al. 2018a, Thellman et al. 2021). Research in recent decades has defied this conception of winter, demonstrating the key role this season plays in natural systems (Cavaliere et al. 2021, Contosta et al. 2020, Cooper 2014, Jones 1999, Kreyling 2020). As a result, numerous studies have focused on defining winter (Contosta et al. 2020, Studd et al. 2021, Sutton et al. 2021), understanding how winters are changing (DeBeer et al. 2021, Rixen et al. 2022), and exploring what these changes portend for future ecosystem form and function (Gordon et al. 2022, Hampton et al. 2017, Kreyling et al. 2011, Pauli et al. 2013, Williams et al. 2018). Much of this research has been biased toward cold, snow-covered regions in the Northern Hemisphere (e.g., Gottlieb & Mankin 2024), with less emphasis on temperate latitudes below 40° north, both in the tropics (e.g., Henry et al. 2022) and throughout the Southern Hemisphere (Ladwig et al. 2016). Prior studies have largely explored the impacts of warming winter temperature and altered precipitation regimes within distinct regions, biomes, or climate zones (e.g., Campbell et al. 2005, Contosta et al. 2020, Cooper 2014, Kreyling 2020) and have focused on individual ecosystem attributes such as soils, vegetation, water, or wildlife (e.g., Henry 2008, Kreyling et al. 2011, Penczykowski et al. 2017, Thellman et al. 2021).

The literature examining the connections and feedbacks among climate change and ecosystem responses is extensive and has explored gradual, linear responses (e.g., Chapin et al. 2004, Hillebrand et al. 2020) as well as radical changes that can be described as tipping points, regime shifts, alternative or multiple stable states, abrupt state changes, and threshold responses (e.g., Grimm et al. 2013, Trisos et al. 2020, Turner et al. 2020). Yet, these investigations have not illustrated how changes during the coldest part of the year may initiate potentially irreversible regime shifts, despite the fact that the duration of the period in which temperatures fall below a particular threshold is important in driving ecosystem form and function (Coulson et al. 2023, Hance et al. 2007, O'Brien et al. 2003, Shugar et al. 2020, Sinclair et al. 2013).

This data-driven literature review builds on the body of knowledge related to our planet's changing climate to both expand the geographical conception of winter and illuminate how threshold changes in winter temperature and precipitation may drive radical and unprecedented shifts in ecosystem form and function due to interactions and feedbacks among winter climate, soils, vegetation, water, and wildlife. We begin by describing the global extent of winter and defining important winter temperature and precipitation threshold conditions, both historically and with worst-case-scenario projections of future climate change. We then show the abrupt, cascading, and potentially irreversible ecological changes, here called threshold responses, that may occur across global biomes when winter temperature and precipitation regimes cross these thresholds.

2. WHERE IS WINTER?

Previous studies have defined winter in a variety of ways, often relying on conditions specific to a study site or broader region (Studd et al. 2021). Some definitions emphasize seasonal differences in solar radiation inputs that result from the axial tilt of Earth as it orbits the sun (Trenberth 1983). Winter is also often defined by its climatic features, such as temperatures below freezing and the presence of ice and snow cover (Contosta et al. 2020). Delineations of winter sometimes focus on biological phenomena, constraining the season to the period when organisms are generally considered to be dormant (Ladwig et al. 2016). Seasonal variation in energy inputs, temperature, and precipitation all affect biological activity, and therefore, common conceptualizations of winter often describe how seasonal changes in temperature and precipitation limit biological processes such as primary production.

Definitions that constrain winter to a period when solar radiation inputs, temperatures, and precipitation together limit biological activity are already implicit in the widely used Köppen–Geiger climate classification system (Köppen 1884). Developed over a century ago, this climate classification system, which has been modified and updated since its inception (e.g., Beck et al. 2018), divides the global land base into five main classes—A, equatorial; B, arid; C, warm temperate; D, snow; and E, polar—based on thresholds of monthly temperature and precipitation. These five classes are further divided by seasonal precipitation patterns and then by seasonal temperature thresholds.

Here, we combine the widely used Köppen–Geiger climate classification system with global, monthly temperature and precipitation data to develop a global understanding of winter conditions. We focus on four main Köppen–Geiger climate zones: B, C, D, and E (we exclude tropical regions in zone A), which are further differentiated by seasonal precipitation and temperature into climate subgroups. While we acknowledge that high altitude areas in tropical regions feature winterlike conditions that occur elsewhere in the world, we omit these areas given the coarse spatial scale of our analysis. For arid climates (Group B), we exclude areas defined as hot (BSh and BWh). For polar climates (Group E), we remove areas classified as ice caps (EF), as these consist of the Antarctic and Greenland ice sheets where biological activity is limited.

Since the dominant vegetation in any biome is constrained by climatic conditions, the Köppen–Geiger system can serve as a proxy for mapping global biomes (Beck et al. 2018). In fact, some biomes occur almost entirely within a single Köppen–Geiger climate zone. For example, tundra biomes are almost entirely in the tundra climate class (ET). Other biomes are distributed across multiple climate zones; midlatitude, temperate forests can occur in both humid subtropical (Cf) and continental (Df) climate zones (Rohli et al. 2015). The variety of biome classification systems (for an overview, see Fischer et al. 2022) further complicates the ability to match specific Köppen–Geiger climate zones to distinct biomes. We assign biomes within the Terrestrial Ecosystems of the World classification system (Olson et al. 2001) to Köppen–Geiger climate zones based on the analysis of Rohli et al. (2015). Within the four major Köppen–Geiger classes (B, C, D, and E) we include in our analysis, we define nine biomes as follows: BWk (deserts); BSk (semiarid grasslands); Cfa, Cfb, and Cfc (warm and subtropical forests); Csa, Csb, and Csc (Mediterranean);

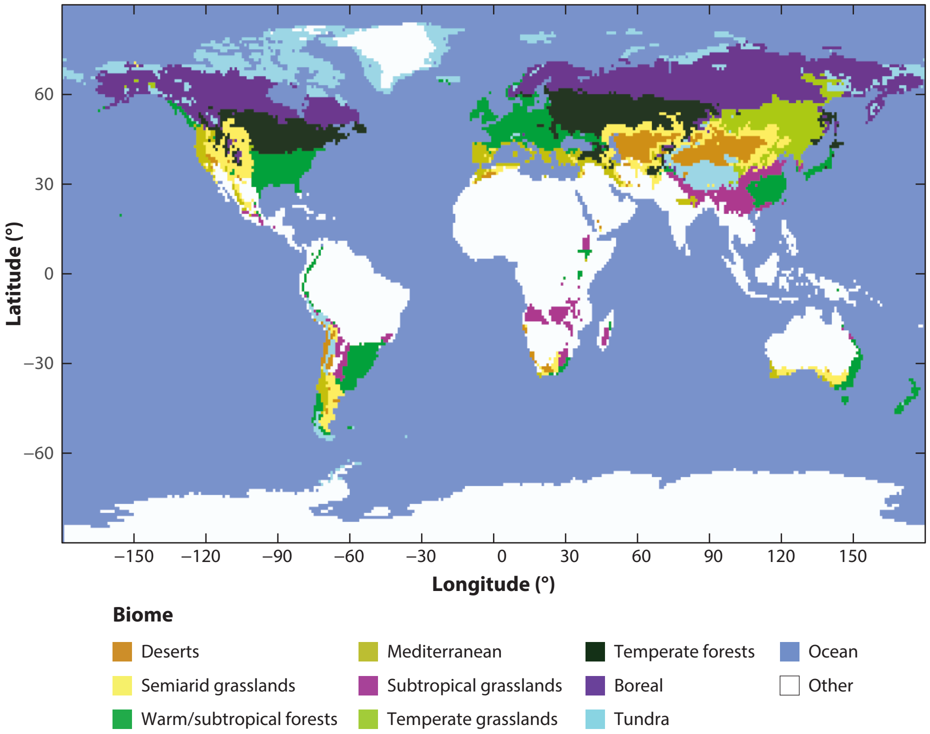

Figure 1

Nine global biomes included in this data-driven review based on current (1951–2000) Köppen–Geiger climate classifications: deserts, semiarid grasslands, warm/subtropical forests, Mediterranean, subtropical grasslands, temperate grasslands, temperate forests, boreal, and tundra.

Cwa, Cwb and Cwc (subtropical grasslands); Dwa, Dwb, Dwc, and Dwd (temperate grasslands); Dfa, Dfb, Dsa, and Dsb (cool temperate forests); Dfc, Dfd, Dsc, and Dsd (boreal); and ET (tundra) (**Figure 1**). Using these nine biome climate groupings, we calculate indicators of winter temperature and precipitation thresholds that, when exceeded, may result in dramatic shifts in ecosystem processes and properties (Hughes et al. 2013, IPCC 2023). Because aquatic ecosystems occur within the terrestrial matrix, we also explicitly explore the effects of threshold changes in winter temperature and precipitation on lakes, particularly within cool temperate areas.

3. DEFINING WINTER THRESHOLD CONDITIONS

Although there is considerable variation in the cold tolerance of life on Earth, −20°C represents a threshold below which many organisms, even insects and prokaryotes, are generally not metabolically active (Bennett et al. 2021, Buckley & Huey 2016), and therefore, for our study, this temperature is an indicator of extreme cold. The freezing point of freshwater (0°C) is another key temperature threshold that determines precipitation phase and affects the likelihood and amount of snow or ice. The freezing point can also act as an important driver of vegetation phenology, often functioning as a baseline for the chilling accumulation requirements for winter dormancy and thermal accumulation needed to break this dormancy (Cook et al. 2012, Wang et al. 2020), though considerable variation exists among species (e.g., Wang et al. 2020). Identifying precipitation thresholds that drive physical responses, such as runoff, or biological phenomena, such as primary production, is less straightforward, as the importance of precipitation phase, timing, and amount varies across biomes and climate zones. Nevertheless, relative changes in total precipitation can show a wet area becoming wetter or a dry area becoming drier (Dore 2005). The proportion of solid (snow) to liquid (rain) precipitation, often called the snow fraction, is also a common metric for describing how the phase of winter precipitation may shift in a changing climate (Feng & Hu 2007).

We use the WorldClimV2.1 global dataset (Fick & Hijmans 2017) to calculate winter temperature thresholds and precipitation conditions described above across nine biome–climate zone groupings (**Figure 1**), during both the historical baseline period (1970–2000) and the future projection range (2081–2100). Data were downloaded at a 10-minute spatial resolution and further downscaled to a 1° spatial resolution using bilinear interpolation to better match the native resolution of many Coupled Model Intercomparison Project Phase 6 (CMIP6) models and to focus on coarse differences between Köppen–Geiger zones. The biome–climate groups are mapped to the climate data using Köppen–Geiger maps from Kottek et al. (2006) that are scaled to a 1° resolution (from a native 0.5° resolution) and reprojected to match the climate data using nearest neighbor methods. We utilize the Intergovernmental Panel on Climate Change Shared Socioeconomic Pathway 5 (SSP585) future projections for the years 2081–2100, which is the high-emission fossil fuel development pathway that yields an additional radiative forcing of 8.5 W/m^2 by 2100 over preindustrial levels (IPCC 2023). We acknowledge that other fossil fuel development pathways are possible and select the SSP585 as a worst-case scenario for changes in important winter temperature and precipitation thresholds that may lead to threshold responses. We calculate the ensemble mean of thirteen downscaled global climate models (GCMs) from CMIP6 under SSP585 for 2081–2100 to determine projections of monthly average minimum and maximum temperatures and total precipitation. The GCMs used from the WorldClimV2.1 dataset are ACCESS-CM2, BCC-CSM2-MR, CMCC-ESM2, EC-Earth3-Veg, FIO-ESM-2–0, GISS-E2–1-G, HadGEM3-GC31-LL, INM-CM5–0, IPSL-CM6A-LR, MIROC6, MPI-ESM1–2-HR, MRI-ESM2–0, and UKESM1–0-LL. These models are chosen as they all have average maximum and minimum temperatures and monthly total precipitation data available for determining historical baseline and future threshold conditions, acknowledging that individual GCMs can overestimate or underestimate observed climate variables and that multi-model ensembles can propagate these uncertainties (Raju & Kumar 2020). Many of the individual models in CMIP6 exhibit a hot-model problem in that they exhibit high climate sensitivity to increased atmospheric carbon dioxide, particularly at the end of the century (Hausfather et al. 2022, Massoud et al. 2023). Thus, the projected changes in winter temperature and precipitation thresholds under SSP585 for 2081–2100 that we present here represent extreme shifts in winter climate conditions.

For potential future temperature thresholds that may affect ecosystem form and function, we determine the probability that mean winter temperature [December, January, and February (DJF) in the Northern Hemisphere and June, July, and August (JJA) in the Southern Hemisphere] is below −20°C or 0°C, both during the reference period and at the end of the century (**Figure 2**). The mean is calculated on a per-pixel basis using the maximum and minimum monthly temperature for the three months of meteorological winter (DJF or JJA). Given the importance of the freezing point of water as both a physical and a biological threshold, we also calculate the duration of the calendar year when maximum temperatures are below 0°C (**Figure 3**) by interpolating the monthly data to a daily scale using a smoothing spline. For winter precipitation in the reference period and under projected climate change by the end of the century, we calculate winter precipitation and winter snowfall totals assuming a phase change threshold of 0°C (**Figure 3**), recognizing that the temperature threshold that delineates rain versus snow can vary between −2°C and 2°C and depends on a variety of complex, interacting factors in the atmosphere

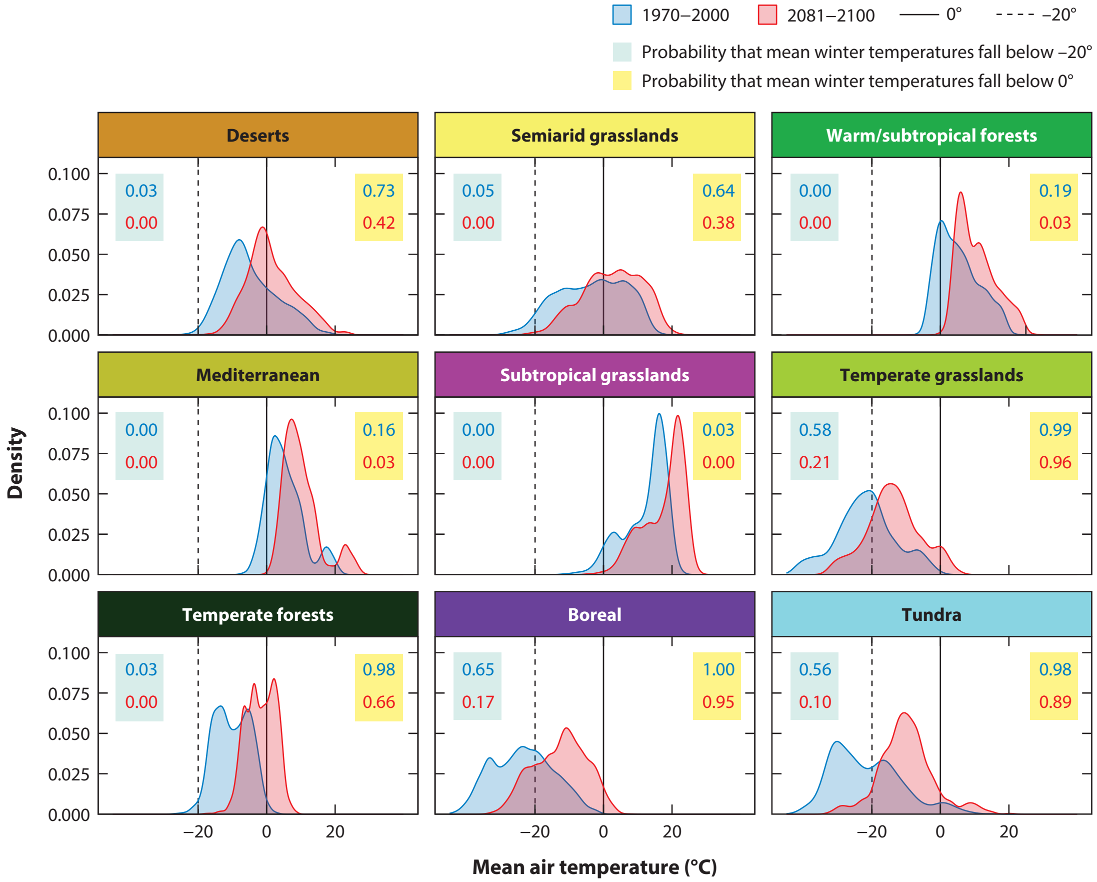

Figure 2

Kernel density plots showing the distribution of mean winter temperatures across nine global biomes during the reference period (1970–2000, *blue*) and with projected future climate change (SSP585 from 2081 to 2100, *red*). Values indicate the probability that mean winter temperatures fall below two temperature thresholds (–20°C or 0°C, as indicated on the left and right, respectively) during 1970–2000 and at the end of the century under the SSP585 scenario. Abbreviation: SSP585, Intergovernmental Panel on Climate Change Shared Socioeconomic Pathway 5.

(Nolin & Daly 2006). Notably, precipitation that falls near the 0°C isotherm may occur as ice pellets, sleet, freezing rain, or freezing drizzle. We do not assign precipitation into any of these mixed precipitation categories given the well-known challenges of now-casting or forecasting them (Minder et al. 2023), though we acknowledge the impacts they can have on both natural and human systems (Groisman et al. 2016). Using the 0°C threshold, the snow fraction is calculated as the ratio of snowfall to total precipitation (Feng & Hu 2007) across each biome. We then estimate relative change (as a percentage) of total precipitation, snowfall, and snow fraction for the winter period between the historical baseline and the end of the century (2081–2100).

4. CROSSING THE LINE: THRESHOLDS AND THRESHOLD CHANGES IN WINTER CONDITIONS

We examine how the loss of winter temperature conditions below certain thresholds (–20°C and 0°C) and altered precipitation regimes (changes in total precipitation, reduced snowfall, and

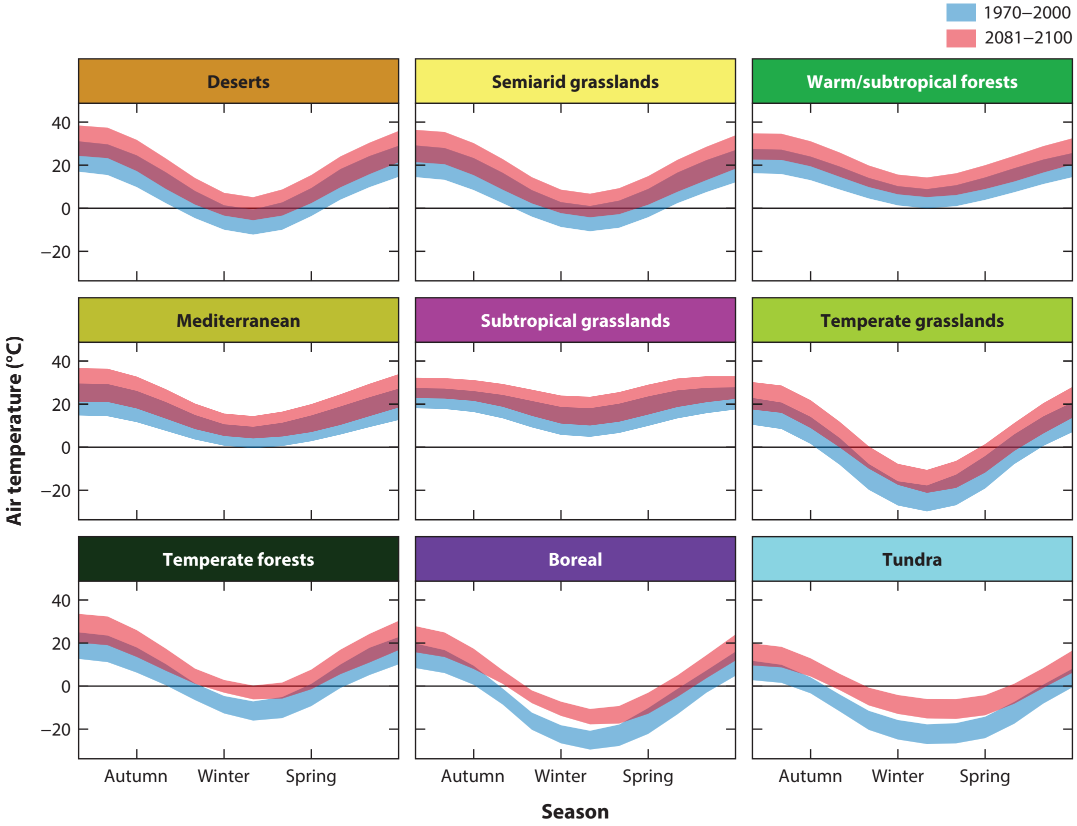

Figure 3

Average monthly minimum temperature (*bottom of each ribbon*) and mean monthly maximum temperature (*top of each ribbon*) across nine global biomes during the reference period (1970–2000, *blue*) and with projected future climate change (SSP585 from 2081 to 2100, *red*). Abbreviation: SSP585, Intergovernmental Panel on Climate Change Shared Socioeconomic Pathway 5.

lower snow fraction) may result in distinct threshold responses within biomes and climate zones. We intend our discussion of threshold responses to changing winter conditions to be illustrative and not exhaustive, recognizing that the changing winter conditions we report for the end of the century represent a worst-case scenario of warming. Given that threshold ecosystem responses may lack historical precedent, we also note that our descriptions of rapid ecological changes due to changing winters are not predictive but instead reflect possible shifts based on current literature and understanding (e.g., Groffman et al. 2006).

4.1. Projected Changes in Winter Temperature and Precipitation

Using winter temperature and precipitation thresholds to determine where and by how much winter conditions may shift, we find that while average winter temperatures vary considerably within and across climate zones, the upward shift of winter temperature distributions indicates that they may be higher at the end of the century (**Figure 2**). Beyond this overall warming trend, temperatures that fall below thresholds of −20°C and 0°C may disappear. The probability that winter temperatures fall below 0°C decreases from ∼0.68 to ∼0.40 in dryland areas (deserts and semiarid grasslands) between the reference period and the SSP585 future climate. Already historically low (probability of 0.03 to 0.19 between 1970–2000), the probability that winter temperatures in

Table 1 Number of days per year when minimum and maximum temperatures are <0°C during the reference period (1970–2000) and with projected future climate change (SSP585 from 2081 to 2100) across nine global climate zones and associated biomes

Biome	# of days T_{min} <0°C		# of days T_{max} <0°C	
	1970–2000	2081–2100	1970–2000	2081–2100
Deserts	156	103	28	0
Semiarid grasslands	159	99	0	0
Warm/subtropical forests	15	0	0	0
Mediterranean	39	0	0	0
Subtropical grasslands	0	0	0	0
Temperate grasslands	236	188	154	116
Temperate forests	184	122	113	0
Boreal	252	197	190	142
Tundra	295	225	225	151

Abbreviations: SSP585, Intergovernmental Panel on Climate Change Shared Socioeconomic Pathway 5; T_{min}, minimum temperature; T_{max}, maximum temperature.

warm temperate and subtropical biomes may be below freezing decreases to near 0 under future climate change. In tundra, boreal, and cool temperate climate zones, the probability that average winter temperatures fall below the −20°C threshold that limits most biological activity decreases from ∼0.50 during the reference period to ∼0.15 in the SSP585 future climate scenario.

Globally, future warming is projected to reduce the duration of temperatures below −20°C and 0°C (**Figure 3**; **Table 1**). Projected climate change entirely eliminates frozen temperatures in warm temperate climate zones that historically experienced mean minimum temperatures close to 0°C during the middle of winter. Semiarid areas lose 2 months of <0°C average minimum temperatures by the end of the century. Below-freezing conditions likewise may contract in desert areas by 2100, with a decrease of 53 days of <0°C average minimum temperatures (from a historical baseline of 156 days) and a loss of all 28 days of <0°C average maximum temperatures. In all other climatic zones, the period with below-freezing temperatures is projected to persist in the future but may occur during fewer months. In snow-dominated, continental climates where temperate grasslands, temperate forests, and boreal forests occur, minimum temperatures <0°C decrease by an average of 55 days. Maximum temperatures <0°C disappear entirely from temperate forests by the end of the century, and tundra regions lose 70 and 74 days with an average minimum and maximum temperature <0°C, respectively.

Relative changes in total precipitation, snowfall, and snow fraction illustrate shifts in the amount and phase of winter precipitation. While the total amounts vary, the biomes featured here are generally projected to experience increases in total precipitation, decreases in snowfall, and decreases in snow fraction (**Figure 4**). The largest projected decreases in snowfall and snow fraction are in places that historically experienced lower snowfall—arid areas and warm temperate climate zones—and likely reflect the loss of below-freezing temperatures.

4.2. Threshold Responses to Changing Winters Across Biomes and Climate Zones

Our analysis of key winter climate indicators illustrates a projected global loss of cold temperatures and precipitation falling as snow under a worst-case scenario of climate change at the end of the century. These projected losses may cause significant ecological changes given the strong controls that temperature and precipitation exert on physical and biological processes. Here, we summarize

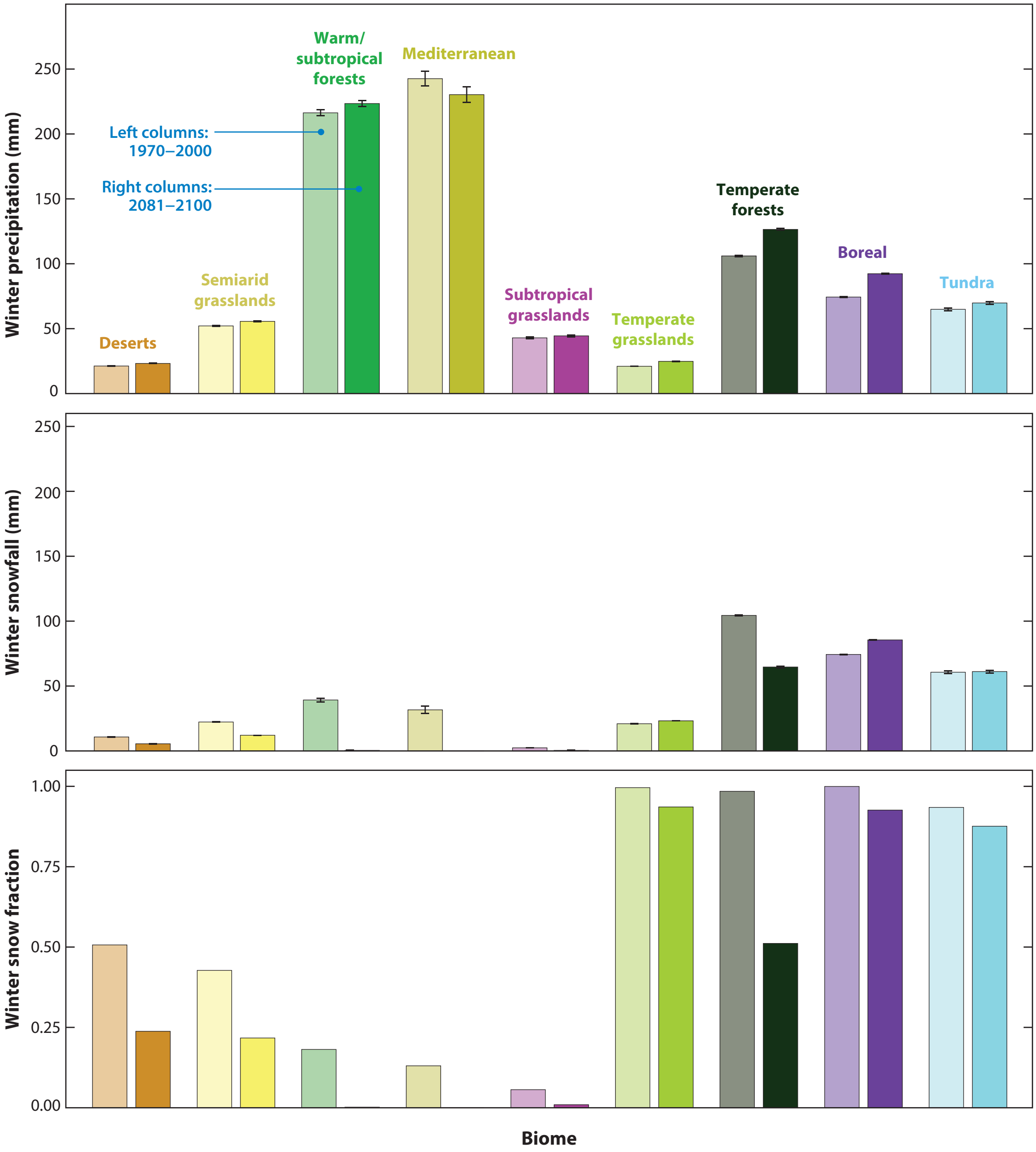

Figure 4

Total winter precipitation, snowfall, and snow fraction across nine global biomes during the reference period (1970–2000; *left columns*) and with projected future climate change (SSP585 from 2081 to 2100; *right columns*). Error bars represent standard errors for winter precipitation and winter snowfall. Winter snow fraction estimates do not include error bars because these values were calculated on a whole biome basis.

possible impacts across four climate zones [dry (B), warm temperate (C), continental (D), and polar (E)] assigned to nine associated biomes (deserts and semiarid grasslands; warm temperate and subtropical forests, grasslands, and Mediterranean biomes; cool temperate forests and grasslands; boreal forests; and Arctic tundra).

4.2.1. Drylands (Climate Classifications BWk and BSk).

Drylands include cold areas of deserts, semiarid grasslands, and steppes and may extend to warm temperate and continental areas that experience dry winters. These regions are on every continent, with areas in western North America, southern Europe, high mountain Asia, and southern South America (**Figure 1**). Mountainous areas in dry climates receive relatively more precipitation and experience colder winters with more snowfall (Sturm et al. 2017) due to both orographic controls and the fact that snowfall is more likely to occur than rainfall in a drier (lower humidity) atmosphere (Harpold et al. 2017). Such mountains therefore provide water to the people that live in these areas (Bales et al. 2006, Barnett et al. 2005). Changes in winter processes in dry regions arise primarily from a loss of snowpack that alters both the timing of water delivery and ecosystem energy budgets.

Changes in the timing of snow water inputs occur due to a changing precipitation phase from snow to rain as well as earlier snowmelt. In arid climates, the probability of mean winter air temperatures occurring below 0°C is projected to change from a probability of ∼0.68 during the reference period to a probability of ∼0.40 under the SSP585 future climate scenario (**Figure 2**). A warming atmosphere is therefore a primary driver of estimated declines in snow fraction of >50% in arid regions (**Figure 4**). The increasing rainfall is typically not stored in the snowpack and enters terrestrial and aquatic systems earlier than snowmelt. Precipitation that continues to fall as snow and is stored as snowpack is expected to melt earlier (Harpold & Brooks 2018) in the winter months before peak snow accumulation and during an earlier start to spring snowmelt freshets. Both increased winter rainfall and earlier snowmelt become potential hazards during wet years (causing winter flooding) and dry years (worsening drought).

In addition to changing the timing and volume of water delivery, changing snow regimes in arid and semiarid areas can impact the snow albedo feedback that is critically important to energy budgets and vapor losses in these dry, water-limited regions (Ban et al. 2023, Milly & Dunne 2020, Walton et al. 2017). Shorter snow seasons are expected to reduce landscape albedo during the winter months, increasing the net radiation available to evaporate water (Walton et al. 2017). The expectation is that accelerating snow albedo feedbacks will reduce streamflow by 5% per degree of warming in places like the western US (Ban et al. 2023) (see the sidebar titled Cascading Impacts of Changing Winters on the Water Budgets of Dry Climates). Both warmer temperatures and earlier melt are expected to initiate earlier growing seasons and intermittent winter transpiration in places

CASCADING IMPACTS OF CHANGING WINTERS ON THE WATER BUDGETS OF DRY CLIMATES

Long-term declines in surface water in arid and semiarid systems are a concern for water resource management. Decreased flows in the Colorado River at Lees Ferry, Arizona, have long been held as an example of climate change impacts on surface water (Hoerling et al. 2019, Udall & Overpeck 2017), with recent modeling suggesting that winter phenomena are primary drivers (Milly & Dunne 2020). Reduced snowmelt water and lower snowmelt rates can decrease the water available for groundwater recharge and streamflow as climate warms. Increases in net radiation from reduced land surface albedo also contribute to reduced streamflow (Milly & Dunne 2020). These reductions in streamflow are occurring simultaneously with landscape-scale tree mortality that would be expected to increase flow due to decreased evapotranspiration (Manning et al. 2022).

that retain leaf area, like conifer forests (Cooper et al. 2020, Winchell et al. 2016). Increases in both albedo and transpiration alter winter and annual water availability and likely increase vegetation water stress later in the growing season (Cooper et al. 2020, Harpold 2016).

Most of the impacts of changing winter temperature and precipitation thresholds on ecosystems and people in dry climates emerge during the summer growing season when systems are most water stressed. Overall increases in vapor losses from a warmer atmosphere and higher potential evapotranspiration (Hammond et al. 2019) (see the sidebar titled Cascading Impacts of Changing Winters on the Water Budgets of Dry Climates) reduce the water that has historically supplied natural and built aquatic systems (Gordon et al. 2022). Combining this with increased human water use and irrigation, streamflow and lake levels are expected to drop and water temperatures to rise from changes in winter processes (Isaak et al. 2010, Sahoo et al. 2011). These changes are likely to have major effects on aquatic biota, including fish (Isaak et al. 2015, Miranda et al. 2020) and freshwater invertebrates and mammals (Ruhí et al. 2013, Sanders et al. 2023). Another consequence of earlier water inputs is increased water stress from a longer growing season (e.g., Harpold 2016, Hu et al. 2010, Winchell et al. 2016).

Although some places may be buffered from water stress due to sufficient precipitation or cooler temperatures (Harpold 2016), most places will see reduced net ecosystem productivity and more water limitations on evapotranspiration (Cao et al. 2022). These water limitations [often expressed as actual evapotranspiration (AET)/potential evapotranspiration (PET) in models] that arise historically during droughts are likely to increase from changes in winter processes. Increased AET/PET ratios are often correlated with increases in forest disturbance from disease, insects, and fire (Westerling 2016). Moreover, a shift away from cold extreme temperatures (<−20°C), as our analysis suggests (**Figure 2**), is likely to allow for increased insect breeding and further positive feedbacks on vegetation disturbance (Mitton & Ferrenberg 2012) that impact wildlife (Ivan et al. 2018). For instance, fewer cold snaps and greater occurrence of drought have increased the likelihood of bark beetle outbreaks in the Rocky Mountains over the past couple decades, causing widespread forest regeneration and browse (food) for herbivores such as elk (*Cervus canadensis*) (Ivan et al. 2018).

Vegetation disturbance and dust transport that occur during summer—in some cases as a result of loss of cold temperatures and snow cover—can also have cascading impacts on snow processes in the ensuing winter. For example, disturbance of desert soils, which can be related to snow-induced drought, increases aeolian dust deposition onto winter snowpacks, decreasing snowpack albedo and hastening snowmelt (Painter et al. 2007, Thind et al. 2019). Forest disturbance feedbacks onto snow processes are more complex. Fire and insect outbreaks propagate black carbon or dead plant material onto the snow surface, decreasing snowpack albedo (Gleason et al. 2013, Koshkin et al. 2022, Winkler et al. 2010). At the same time, the loss of forest canopy cover can increase albedo at the landscape scale (Baker et al. 2017).

4.2.2. Warm temperate areas (Climate Classifications Cs, Cf, and Cw). Warm temperate and subtropical areas are distributed around the globe, with Mediterranean climates (Cs) occurring along the southwest coasts of all continents except Antarctica, humid subtropical climates (Cf) generally found on the eastern coasts of continents, and dry winter climates (Cw) in areas dominated by monsoons. No single global biome sits within these Köppen–Geiger zones, though grasslands and subtropical shrublands occur in areas within dry summers (Cs) and dry winters (Cw), while subtropical forests occur in places without a seasonal dry season (Cf) (Rohli et al. 2015) (**Figure 1**). These warm temperate climates historically feature average temperatures above −3°C during the coldest month of winter, though minimum temperatures can be lower than this threshold during brief periods. Projected winter climate change throughout warm temperate biomes features the complete disappearance of cold temperatures, including those below freezing, by the end of the century under the worst-case scenario of greenhouse gas emissions (**Figures 2** and **3**). A key impact of the loss of these below-freezing temperatures is the tropicalization of temperate areas—a process by which species adapted to hotter climates are able to move poleward in the absence of cold conditions that cause physiological stress (Vergés et al. 2014). The chilling required to induce this stress is context specific and can vary across life stages, individuals, and species (Osland et al. 2021). It may occur during low-temperature excursions with frequent enough return intervals to induce physiological damage and mortality, or it may be the result of average winter minimum temperatures that exceed organism-specific chilling thresholds (Jalili et al. 2010, Osland et al. 2021). Although it is more pronounced in marine and coastal wetland environments than upland areas (Lenoir et al. 2020), terrestrial ecosystems at the tropical–temperate interface are also experiencing this phenomenon, with implications for ecosystem function that are poorly understood (Osland et al. 2021).

In drier places, like highlands and subtropical grasslands as well as warmer areas of semiarid grasslands, freeze events limit the distribution of woody tropical vegetation (Bojórquez et al. 2019) that could expand poleward (or upward in elevation) with the loss of cold winter temperatures (Osland et al. 2021, Tikkanen et al. 2021). Milder, warmer, and wetter winters can also interact with the escape of introduced species to accelerate the process of tropicalization and its impacts (Osland & Feher 2020, Osland et al. 2023). In arid regions of the southwestern US, the northward advancement of introduced tropical grasses for grazing is already occurring. Buffelgrass (*Pennisetum ciliare*), a species originally from tropical and subtropical grasslands of Africa and western Asia, is projected to expand northward across areas of the Sonoran Desert as winters become warmer and wetter, outcompeting endemic species, altering ecohydrology, and increasing the length and intensity of the wildfire season (Abatzoglou & Kolden 2011).

In more humid areas of the warm temperate climate zone, warm-adapted reptiles such as the American crocodile (*Crocodylus acutus*) and tropical amphibians such as the Cuban treefrog (*Osteopilus septentrionalis*) are expected to move poleward with the removal of cold temperature constraints (Haggerty & Crisman 2015, Mazzotti et al. 2016, Osland et al. 2021). As in arid regions, the loss of cold conditions can combine with the introduction of nonnative species, resulting in the range expansion of tropical invasives into warm temperate areas. Florida, a state in the southeastern US, is a global hotspot for this phenomenon (Osland et al. 2023) and is experiencing the proliferation of invasive reptiles such as the Burmese python (*Python bivittatus*) (Mazzotti et al. 2011) as well as the expansion of invasive woody plants like the Brazilian pepper (*Schinus terebinthifolius*) (Osland et al. 2020).

4.2.3. Cool temperate forests and grasslands (Climate Classifications Dwa, Dwb, Dwc, Dfa, Dfb, Dsa, and Dsb). Cool temperate forests and grasslands fall within the hot or warm summer continental and hemiboreal climate zones and include cool temperate forests and grasslands, though no single climate zone comprises the majority of these biomes (Rohli et al. 2015) (**Figure 1**). In these areas, minimum winter temperatures that exceed 0°C are projected to increase from 155 days in the years 1970–2000 to 210 days in the years 2081–2100 under SSP585 (**Figure 3**; **Table 1**), and the fraction of precipitation expected to fall as snow in continental climates is projected to decrease by 10–50% by the end of the century (**Figure 4**). This loss of winter snowpack and increased winter temperatures, particularly above 0°C, are the key threshold changes in winter climate in cool temperate ecosystems (e.g., Contosta et al. 2020) that are likely to drive threshold changes in soils, vegetation, wildlife, and their interactions. Aquatic ecosystems that occur in these biomes are also likely to experience significant impacts in the absence of freezing conditions that both allow for seasonal ice cover to form and persist and drive seasonal patterns in runoff timing and volume.

Winter soil biogeochemical properties and processes are moderated by the depth and duration of snow cover in temperate forests and grasslands. Snow insulates soil from fluctuating atmospheric conditions (Edwards & Cresser 1992) and thus keeps soil temperatures at or above 0°C and water in liquid form (Sharratt et al. 1992). A more shallow, intermittent snowpack can result in increased frequency and intensity of soil freeze–thaw cycles if air temperatures fall below and then rise above the 0°C threshold (Groffman et al. 2001, Henry 2008). Previous studies have observed increasing (Henry 2008) or decreasing (Peng et al. 2017) depth or duration of soil frost with changing winter climate in cool temperate areas. The magnitude and direction of freeze–thaw depends on geographic location and the complex interaction between air temperature and snow depth in driving soil microclimatic conditions (Hatami & Nazemi 2022).

The loss of insulating snow and fluctuation of soil temperatures above and below freezing can directly impact vegetation through damage to fine roots (Pauli et al. 2013). Alaskan yellow cedar (*Callitropsis nootkatensis*), a culturally, economically, and ecologically important conifer species in coastal temperate rainforests of North America, is particularly susceptible to this kind of freezing injury (Hennon et al. 2012). Likewise, deciduous trees, including those endemic to the northeastern US such as sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*), are vulnerable to loss of snowpack (Campbell et al. 2014, Tierney et al. 2001). The depth and duration of winter snow cover can also indirectly affect vegetation by driving spatial and temporal variation in water and nutrients, particularly in grasslands (Yano et al. 2015). A deep and long-lasting snowpack drives water and nutrient availability at the start of the growing season (Li et al. 2020). When combined with increased risk of fine root mortality, the shallow, intermittent snow cover expected in future winters can result in lower vegetation productivity during the ensuing growing season as fewer fine roots confront reduced water and nutrient resources in grasslands (Kreyling et al. 2019) or are damaged from the previous winter's soil frost (Reinmann et al. 2019).

Aboveground, warmer winter temperatures, particularly those above freezing, can also have complex effects on vegetation. Winter warming and the accumulation of growing degree days can result in earlier green-up of herbaceous plants such as wildflowers and grasses (Cayan et al. 2001), as well as coniferous trees whose growth can be constrained by low temperatures (Lebourgeois et al. 2010, Song et al. 2021). However, the contraction of the cold period below zero and the loss of freezing temperatures can also delay the onset of the growing season for some grassland and deciduous broadleaf species that must meet physiological chilling requirements before responding to warming temperatures in late winter and early spring (Polgar et al. 2014, Zeeman et al. 2017). Further, herbaceous and woody species that emerge from dormancy in the wake of warmer winters and springs are also at risk of experiencing frost injury if temperatures fall back below freezing, as is projected for many areas within this climate zone (Gallinat & Primack 2016). Warming winters and loss of snow also damage roots and delay leaf-out of maple saplings (Sanders-DeMott et al. 2018b). Yet, reduced winter snow cover and the resulting increase in soil freeze–thaw cycles can reduce rates of stem herbivory in winter, offsetting some of the damage caused to sapling roots in winter (Sanders-DeMott et al. 2018a).

The impact of warming winters is less clearly detrimental to animal species in temperate systems. Declines in snowpack have reduced the ability of trailing edge populations of winter-adapted species such as ruffed grouse (*Bonasa umbellus*) and snowshoe hares (*Lepus americanus*) to maintain a survival advantage either directly or indirectly (Shipley et al. 2020, Zimova et al. 2016). On the other hand, some hibernating species are able to feed longer and hibernate for a shorter period of time [e.g., tree-roosting bats (Turbill 2008)]. Reduced snowpack has been shown to have a positive effect on European bison (*Bison bonasus*) in the temperate forests of Poland through increased mobility and decreased rates of parasitism from less supplementary feeding of animals during winter (Bramorska et al. 2023). However, increased mobility can have a negative impact on plant communities and lead to nuisance problems with farmers (Bramorska et al. 2023). Changes in snowpack dynamics also influence community interactions and potentially ecosystem processes. For example, warming winters and reductions in snowpack are thought to favor white-tailed deer (*Odocoileus virginianus*) but not moose (*Alces alces*) (Weiskopf et al. 2019), which could have cascading impacts on forested ecosystems, as these keystone herbivores have distinct browse preferences (Groffman et al. 2012). Further, the combination of reduced snow depth and duration and lower moose abundance can alter nutrient cycling via complex pathways (Christenson et al. 2010).

4.2.4. Loss of freshwater ice as a leading indicator of changing winters.

Changes in lake ice cover are strongly driven by losses of below-freezing air temperatures that are already underway and are projected to continue in cool temperate biomes (e.g., **Figures 2** and **3**), though factors such as wind and lake morphometry also play a role (Maberly et al. 2020). Freshwater lakes across cool temperate regions are increasingly experiencing years with no ice cover (Filazzola et al. 2020) or are showing trends toward shorter ice duration in boreal and tundra areas (Huang et al. 2022, Imrit & Sharma 2021, Sharma et al. 2021). This loss of lake ice is a key indicator of changing winter climate globally (Adrian et al. 2009, Woolway et al. 2020) and carries consequences for the biology, chemistry, and physics of lakes as well as for freshwater resources more generally (Woolway et al. 2020). In addition to the direct impacts of lake ice loss, the decline or disappearance of below-freezing conditions (**Figures 2** and **3**) can indirectly impact lake water and chemical budgets due to shifts in watershed vegetation, soil, and runoff processes (e.g., Hobbie & Chapin 1996, Inamdar et al. 2018, Seybold et al. 2022).

There are multiple ways in which changing winter climate may induce threshold changes in lakes (e.g., Cavaliere et al. 2021, Mueller et al. 2009, Rühland et al. 2015, Williamson et al. 2009, Woolway et al. 2022). In regions with historically long durations of ice cover (e.g., boreal and tundra biomes), the decline in the frozen period (**Figure 3**) that limits gas exchange will lead to a contraction or complete disappearance of anoxic winter conditions in shallow lakes (Cavaliere & Baulch 2019, Fang & Stefan 2009, Mathias & Barica 1980, Meding & Jackson 2003). This naturally occurring anoxia leads to the death of key species, including some fish, with effects that may propagate through food webs (Tonn & Magnuson 1982, Welborn et al. 1996). Anoxia can also lead to altered biogeochemical cycling, including greater nutrient release from sediments (Schroth et al. 2015). Systems that no longer experience anoxia (a threshold change) are at risk of irreversible ecological change, propagated via bottom-up impacts on nutrient availability and top-down effects via return or expansion of anoxia-sensitive species.

The end of winter lake ice can also alter energy inputs and mixing dynamics in many temperate lakes. Rapid loss of below-freezing air temperatures (**Figure 2**) will bring the end of ice cover to many cool temperate lakes (Huang et al. 2022). This change will increase light inputs to the lake surface and alter mixing dynamics (Cavaliere et al. 2021), particularly the loss of inverse stratification that occurs in winter (Woolway et al. 2020, 2022). Complex and variable changes in the physical environment may result for phytoplankton, with the potential for changes in community composition and primary productivity, depending on water column mixing depths and other factors (Cavaliere et al. 2021, Pernica et al. 2017, Weyhenmeyer et al. 2008). The lack of ice through winter can also lead to an extended period where winds can resuspend benthic sediments in shallow areas, altering turbidity, light, and nutrient availability (Kleeberg et al. 2013, Niemistö & Horppila 2007).

Changes in the timing, volume, and chemistry of winter runoff can also impact lakes. Winter-related changes in watershed hydrology, soils, vegetation, and their interactions can alter the loads and concentrations of dissolved organic carbon, nutrients, and contaminants, and their pH (Casson et al. 2012, Sickman et al. 2003), sometimes in rapid and nonlinear ways (Inamdar et al. 2018, Matzner & Borken 2008). This is especially the case as climate transitions through winters that touch or straddle the zero-degree isotherm (**Figures 2** and **3**), in which freeze–thaw cycling can increase nutrient release from surrounding uplands (e.g., Inamdar et al. 2018, Rixen et al. 2008) and rain-on-snow events induce large pulses of water and nutrients (Casson et al. 2010, Seybold et al. 2022). A state change in lakes from a lower-productivity state (nutrient poor conditions) to one richer in nutrients and algae (or cyanobacteria) has been commonly observed (Gilarranz et al. 2022, Scheffer et al. 1993). Changes in winter anoxia, energy inputs, mixing dynamics, and watershed biogeochemistry that result from changing winter temperatures together increase the risk of driving a shift in the trophic state of lake ecosystems in cool temperate biomes.

4.2.5. Boreal forests (Climate Classifications Dfc, Dfd, Dwc, and Dwd). Boreal forests overlap with ~70% of Köppen–Geiger climate zones classified as subarctic or boreal climates (Rohli et al. 2015) (**Figure 1**). These areas historically experience a prolonged period (252 days) of minimum temperatures <0°C (**Figure 3**; **Table 1**) and high snowfall rates of ~75 mm per year (**Figure 4**). While models of winter in the boreal forest biome project a contracting dormant season of below-freezing temperatures and decreasing snowfall and snow fraction (**Figures 3** and **4**), the most profound change to boreal winters may be the disappearance of extremely cold winter temperatures of <−20°C (**Figure 2**). In this region, extreme cold temperatures pose physiological challenges to organisms and constrain productivity, species ranges, and growth rates. The loss of extreme cold, both alone and in combination with decreasing snowfall, impacts individual and interacting components of boreal forest ecosystems.

Soils in the boreal region store vast amounts of carbon, with estimates of up to 50% of the global soil organic carbon stock (Ciais et al. 2010, Malhi et al. 1999), and are sensitive to changes in climate, particularly as up to 80% of boreal forests globally are underlain by permafrost (Helbig et al. 2016). As in temperate climate zones, snowpacks insulate soils and decouple soil temperature from air temperature across most of the boreal region for much of the winter, and thus many of the changes to soil during the winter season depend on the duration and extent of snow cover (Jungqvist et al. 2014). Climate models project that increases in winter soil temperatures will not be uniform across the landscape; riparian areas and waterlogged soils may warm faster than upland or well-drained sites, and changes may be most pronounced at the end of winter (Fan et al. 2011, Oni et al. 2017). Warmer soils can lead to increases in nutrient and water availability, which can stimulate increased decomposition and aboveground biomass accumulation in the short term, although this effect may not be sustained at decadal timescales when other factors such as moisture and nitrogen availability may limit these processes (Lim et al. 2019).

Warmer winter temperatures and shorter snow-covered seasons can also directly impact boreal vegetation. Snow that falls at warmer temperatures tends to be heavier, and an increase in this kind of precipitation can damage trees, leading to decreased yields from forestry operations and potential impacts to power lines (Lehtonen et al. 2016). The loss of extremely cold temperatures can shift forest community composition; for instance, a decrease in exposure to cold temperatures may improve the growth of pines and high-elevation conifers across Canada while negatively affecting the growth of common angiosperms, especially those with early spring leaf-out (Girardin et al. 2022). Many boreal tree species are distributed throughout the expanse of the boreal region, conferring some resilience on the ecosystem as individual species ranges shift with warmer temperatures (Price et al. 2013). Changing winter conditions can affect disturbance regimes in boreal forests; an earlier start and a later end to fire season, coupled with drier summer soils as a result of reduced snowmelt, can increase fire activity (Kim et al. 2020). The removal of lower lethal temperatures for insect pests allows for the proliferation of the mountain pine beetle (*Dendroctonus ponderosae*) and the expansion of eastern spruce budworm (*Choristoneura fumiferana*) (Pureswaran et al. 2015). The interaction of changes to insect outbreaks and fire regimes may result in a cascade

THE LOSS OF EXTREMELY COLD TEMPERATURES IN THE BOREAL ZONE MAY ALTER FEEDBACKS AMONG INSECTS, DEFOLIATION, AND FIRE REGIMES

Increasing winter temperatures can allow insects to expand their ranges but can also cause mismatches between bud break and larval hatching (Johnson et al. 2010, Pureswaran et al. 2018). In North America, climate impacts on spruce budworm dynamics are well studied, as its outbreaks, which are increasing in severity, cause massive ecological impacts (Gray 2008). Historically, black spruce (*Picea mariana*) has not been a desirable host species for spruce budworm, both because it dominates at higher latitudes where winters are longer and because its budburst is later than that of balsam fir (*Abies balsamea*) and thus is mismatched with larval emergence timing (Pureswaran et al. 2015). As the range of the spruce budworm expands northward and black spruce budbreak moves earlier in the season, there is potential for regions that have not experienced significant outbreaks to be affected. Defoliated trees are good fuel for fires, and therefore, outbreaks can result in shortening fire cycles in boreal forests (Fleming et al. 2002). As shorter, drier winters also increase fire risk in the subsequent summer, there is the potential for both direct and indirect effects of winter climate change on fire regimes. The combination of increased spruce budworm outbreaks and shorter fire cycles may result in long-term changes to forest composition, but the trajectories are nonlinear and depend on multiple factors (Pureswaran et al. 2015).

of ecosystem consequences (see the sidebar titled The Loss of Extremely Cold Temperatures in the Boreal Zone May Alter Feedbacks Among Insects, Defoliation, and Fire Regimes).

Boreal animals, which are mostly cold adapted, are expected to see large negative impacts from waning winters. Boreal forest birds have experienced the second largest losses (after grassland birds) in North America in the last half century (Rosenberg et al. 2019) and are projected to see major range shifts in the future (Virkkala et al. 2008). Range expansion of temperate species is likely to alter competition and predation (Wallingford et al. 2020), changing food webs and ecosystem energy flows. In turn, boreal species are displacing Arctic species (Kortsch et al. 2015, Wallingford et al. 2020). Loss of snowpack may have a large impact on the uniquely adapted life history of boreal species, disrupting the refrigeration of food by wolverines (*Gulo gulo*), Canada jays (*Perisoreus canadensis*), and Eurasian pygmy owls (*Glaucidium passerinum*) (Inman et al. 2012, Masoero et al. 2020, Sechley et al. 2015) and the subnivium habitats of small mammals (Scott et al. 2022), while reducing survival of alpine butterflies (Roland & Matter 2016). Increased forest fires (due to increased temperatures) are projected to reduce important winter food resources, such as lichen for caribou (*Rangifer tarandus*) in northern boreal forest regions, causing a decline in caribou populations (Gustine et al. 2014).

4.2.6. Arctic tundra (Climate Classification ET). Although alpine tundra comprises a small portion of the tundra climate zone, 81% of the ET intersects with the Arctic tundra biome (Rohli et al. 2015), and thus we focus on threshold conditions and threshold changes in Arctic tundra systems here. Arctic tundra is located in the northernmost areas of the Northern Hemisphere that are not covered with ice sheets. Winter can comprise up to nine months of the year in this biome, beginning with the onset of persistently frozen or snow-covered ground and ending with snowmelt (Cooper 2014). This extended period of cold temperatures is already contracting and is projected to become even shorter by the end of the century (**Figure 3**), since Arctic warming, which is occurring at two to four times the global average (Rantanen et al. 2022), is especially pronounced in winter (Bintanja & van der Linden 2013, Rantanen et al. 2022). Arctic regions are also already experiencing increased precipitation (Walsh et al. 2022), and this trend is projected to continue (**Figure 4**). Higher precipitation during winter months may manifest as higher snowfall totals if temperatures stay below freezing even as they warm (**Figure 4**). However, the snow fraction is expected to decrease over the Arctic (**Figure 4**), with most of the snow loss in the autumn months (McCrystall et al. 2021). Thus, while meteorological winter is expected to remain below freezing, key threshold changes in Arctic tundra systems include delayed onset of the cold, a shorter snow-covered period, earlier snow melt, and deeper snow cover during the core of the winter season. Together these phenomena impact ground-thermal regimes, vegetation, snow-adapted wildlife, and the interactions among them (Rixen et al. 2022).

The later onset of the Arctic winter can result in the extension of the zero-curtain period, in which the active layer stays unfrozen for longer (Arndt et al. 2019, Commane et al. 2017). This can increase carbon emissions from permafrost soils as both carbon dioxide and methane (Arndt et al. 2019, Commane et al. 2017), resulting in positive climate forcing, and may also alter soil microbial community composition and function by supporting increased nitrogen mineralization and microbial growth throughout winter (Grogan & Jonasson 2003). Once a snowpack develops, it insulates soil from fluctuating air temperatures, even extremely cold ones, so long as it reaches a minimum depth of 25 to 50 cm (Slater et al. 2017). Increased snow depth can result in warmer soil temperatures and thus higher microbial activity during winter, which in turn, can increase nutrient content (Larsen et al. 2007). Snowmelt is one of the most dynamic periods in soils in the Arctic, with quickly declining microbial biomass reported across the pan-Arctic (Edwards & Jefferies 2013, Poppeliers et al. 2022, Sistla & Schimel 2013). Thus, earlier snowmelt could potentially alter biogeochemical cycling and even growing season processes by altering microbial community development and nutrient availability throughout the year.

The shortening of the Arctic winter can also manifest as earlier spring green-up and delayed autumn senescence of tundra vegetation (Ernakovich et al. 2014). However, warmer and shorter winters may not always result in longer growing seasons, and loss of snowpack in the face of cold temperatures can stress plants (Slatyer et al. 2022). Earlier plant senescence can also occur following advanced snowmelt (Livensperger et al. 2019), which may be due to warmer, drier conditions during the spring and summer that reduce plant productivity (Zona et al. 2023). Milder conditions year-round also allow for the poleward expansion of deciduous woody shrubs (Elmendorf et al. 2012, García Criado et al. 2020, Mekonnen et al. 2021, Myers-Smith et al. 2011), though shrub encroachment into Arctic tundra varies as a function of snow depth and snow disappearance date, soil moisture availability, topography, and permafrost thaw depth (Mekonnen et al. 2021). This shrubification of the Arctic can interact with increased snow cover to affect ground thermal regimes, the surface energy balance, and snow-adapted mammals, resulting in a positive feedback that manifests as a novel ecosystem (Sturm et al. 2001) (see the sidebar titled Feedbacks Among Increased Snow Depth, Expanded Shrub Cover, and Altered Grazing Regimes Could Create Novel Arctic Ecosystems).

Arctic animals are considered highly vulnerable to the shortening of the cold, snowy period, particularly snow-adapted species (Woo-Durand et al. 2020). The loss of snowpack negatively affects species that overwinter in the subnivium (Pauli et al. 2013). Warmer winters are contributing to the expansion of species from lower latitudes into the Arctic, including predators (Dalerum et al. 2017, Gallant et al. 2020) such as gray wolf (*Canis lupus*) (Dalerum et al. 2017) and red fox (*Vulpes vulpes*) (Gallant et al. 2020, Van Hemert et al. 2014). Warmer, earlier springs can cause species such as Arctic ground squirrels (*Urocitellus parryii*) to come out of hibernation earlier, resulting in phenological mismatches between squirrels and their food sources (Kubelka et al. 2022, Wheeler & Hik 2013). Later snowpack onset and earlier melt are also projected to increase predation on resident species like the collared lemming (*Dicrostonyx groenlandicus*) (Duncan et al. 2021). Declines in late winter snow depth may also increase the overlap of diets among rock ptarmigan (*Lagopus mutus*), musk ox (*Ovibos moschatus*), and Arctic hare (*Lepus arcticus*), thereby increasing competition for food (Schmidt et al. 2018). Shifting phenology of Arctic wildlife can also interact with changes

FEEDBACKS AMONG INCREASED SNOW DEPTH, EXPANDED SHRUB COVER, AND ALTERED GRAZING REGIMES COULD CREATE NOVEL ARCTIC ECOSYSTEMS

The positive feedback between increased shrub abundance and changing snow depth, or the snow–shrub hypothesis of Sturm et al. (2001), states that by trapping snow, shrub canopies insulate soil during winter. This makes conditions more favorable for faster rates of nutrient cycling that then support higher shrub growth rates during the ensuing growing season (Hollesen et al. 2015), although this is not always the case (Frei & Henry 2021). The proliferation of deciduous shrubs can affect plant–herbivore interactions because rodents and smaller-bodied mammals prefer mosses and dwarf shrubs that may be shaded out as larger deciduous shrubs expand across the biome (Mekonnen et al. 2018). Larger herbivores such as reindeer and caribou prefer the deciduous shrub species that are advancing northward across the Arctic tundra (Klein 1968, Ricca et al. 2016), yet grazing pressure can also reduce shrub abundance (Kitti et al. 2009, Olofsson et al. 2001), suggesting that herbivores should be considered as part of a snow–shrub grazing feedback that may drive fundamental changes in ecosystem form and function.

in plant phenology, vegetation composition, snow cover, and soil physicochemical processes (see the sidebar titled Feedbacks Among Increased Snow Depth, Expanded Shrub Cover, and Altered Grazing Regimes Could Create Novel Arctic Ecosystems). Indeed, some of these changes are projected to disrupt continental processes of migration (Kubelka et al. 2022).

5. SUMMARY

5.1. Unanswered Questions and Future Research Directions

5.1.1. Winter climate processes. Several key uncertainties in future winter climate could have large implications for ecological responses. First, changes in winter precipitation are very uncertain in most of the midlatitudes. Areas where future precipitation could increase or decrease require better modeling to constrain future winter processes (Poujol et al. 2021, Shepherd 2014). In addition to volume, an improved ability to estimate precipitation phase, particularly mixed precipitation, is particularly important in areas where temperatures will straddle the 0°C isotherm (Jennings et al. 2018). Second, humidity is generally accepted to increase globally, but many of these processes are not simulated well by GCMs and can have large impacts on winter energy budgets and snowpack change (Harpold & Brooks 2018, Sumargo & Cayan 2018). Similarly, changes in wind speeds and storm tracks are not simulated well by GCMs and can have dramatic effects on snowpack and precipitation processes (Luce et al. 2013) that affect ecosystem form and function.

5.1.2. Mountain processes. Mountains are subject to uncertain climate feedbacks that remain difficult to predict with current GCMs. First, changes in orographic precipitation from altered storm tracks, reduced wind speeds (Luce et al. 2013), or changes in precipitation phase from snow to rain (Minder & Kingsmill 2013) are challenging to simulate in the future. Resolving precipitation in mountain areas is a known limitation of GCMs that typically requires dynamical downscaling. It is also expected that elevation-dependent temperature increases will cause accelerated warming at high elevations (Pepin 2015, Pepin et al. 2022), but the strength of that signal and its geographic variability are not well known. The effects of accelerated warming and altered precipitation regimes on winter-adapted plants and animals are likely to cause local extirpations or extinctions (especially of endemic species) in montane areas (Billman et al. 2021, Freeman et al. 2021), but there is considerable uncertainty due to many exogenous (e.g., habitat recovery, topography, biotic interactions) and endogenous (e.g., dispersal ability) factors (Deluca & King 2016, Elsen & Tingley 2015).

5.1.3. Uncertain processes in the North. With northern environments warming at rates three to four times faster than those of the rest of the world (Rantanen et al. 2022), these ecosystems are important environments in which to direct future research. Most GCMs do not accurately account for permafrost thaw (Schädel et al. 2024), and indeed, much work is needed to improve our understanding of altered microbial dynamics, shifting snowpack, and changes to periods of unfrozen ground. All these factors can impact biogeochemical cycles and disturb current vegetation regimes. Further, more information is needed on how winter rain-on-snow, and episodic snow-ice melting events impact wildlife and fish populations that are vital to ecosystem function, Indigenous ways of life, and northern economies (Gladun et al. 2021). Abiotic factors such as deep snow mediate biotic interactions and are important for maintaining species range limits (Sirén & Morelli 2020). As such, milder winters may increase competition and predation and cause rapid range shifts (Zimova et al. 2016); however, there are other factors such as habitat availability (Sirén & Morelli 2020) that complicate our ability to predict the rate of distributional shifts and their cascading impacts on ecosystem function.

5.2. Conclusions

Our analysis of key winter temperature and precipitation threshold conditions under a worst-case scenario of climate change shows a projected loss of extreme cold and below-freezing temperatures, a contraction of the period of the year that exhibits temperatures <0°C, an increase in winter precipitation, and a decrease in snow fraction. The loss of extreme cold may be most pronounced in Arctic tundra and both boreal and cool temperate regions, where the probability of winter temperatures being <−20°C is projected to decrease substantially between the reference period and possible future climate change under SSP585. While Arctic and boreal regions are projected to largely retain temperatures below 0°C during winter, they may experience an ∼23% decrease in the number of days that minimum temperatures are <0°C throughout the year. We observe the most prominent potential loss in frozen conditions in warm temperate climates. Arid and semiarid areas fall somewhere in between, with projected losses of ∼56 days of the year with <0°C minimum temperatures and a probability of temperatures going below freezing in the winter decreasing from ∼0.70 to ∼0.40 by 2100. Possible reductions in below-freezing temperatures everywhere likely explain projected decreases in snow fraction. We observe the largest possible losses in snowfall in the places that also exhibit substantial declines in below-freezing temperatures, with dryland systems potentially losing 50% of snowfall that occurred during the reference period and warm temperature systems potentially losing 100% of snow with a worst-case scenario of future climate change.

We interpret these projected changes in winter threshold conditions by synthesizing the current literature on how changing winters are already affecting or may impact ecosystems across the Earth. Some consequences of the loss of extreme cold or below-freezing temperatures are ubiquitous; everywhere species ranges are expanding poleward with the disappearance of lower lethal temperatures. These range expansions include species at multiple trophic levels, from vegetation through apex predators, and often result in altered food web dynamics, elevated mortality, and shifts in disturbance regimes. Declines in cold temperatures and snow cover also exert uneven impacts among species, with some organisms thriving and others declining with milder winter conditions. We also highlight unique threshold responses within climate zones and associated biomes that may result in irreversible regime shifts. These include loss of snow in dryland areas that rely on high-elevation water towers for hydrologic resources, tropicalization of warm temperate regions, increased freeze–thaw in temperate forests and grasslands, increasing forest pest outbreaks in boreal areas, and shrubification in the Arctic. Each of these phenomena includes positive feedbacks, either during winter or throughout the rest of the year, that reinforce the threshold responses. We note that impacts on aquatic environments such as lakes are leading indicators of changing winters across the globe, particularly in cool temperate areas where freeze–thaw conditions straddle the 0°C isotherm and can push previously frozen lakes into an ice-free condition. Aquatic ecosystems such as lakes can also act as sentinels for the disappearance of important winter thresholds. As receiving bodies, they integrate the effects of changing winters on upland watersheds.

We acknowledge that the global scope and coarse spatial scale of this data-driven review obscures finer scale impacts of changing winters on some regions, particularly higher elevation areas whose microclimatic conditions may not align with the assigned Köppen–Geiger climate zones. In addition, while the Köppen–Geiger classification system can be used as a rough proxy for the distribution of global biomes, not all biomes fit cleanly into a climate zone or vice versa. Further, we realize that our selection of models to include in the ensemble means of future temperature and precipitation thresholds under SSP585 likely introduces uncertainty into the occurrence of winter thresholds at the end of the century. We recognize all of these issues and note that the goal of our data-driven review is not to predict but to illustrate the occurrence of winter threshold conditions, now and with potential future climate change. We aim to describe how the loss of these threshold conditions may have irreversible and cascading impacts on ecosystems across the globe. We do this in the knowledge that our portrayal of threshold changes and their impacts illuminates a possible but not inevitable worst-case scenario of climate change. Policy decisions can help to avoid this scenario, even as management priorities can conserve areas that act as climate refugia because winter conditions are not projected to exceed critical thresholds (Stralberg et al. 2020).

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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