A systematic quantitative review of ecological responses to variation in seasonal snow cover

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Abstract

Seasonal snow is among the most important factors governing the ecology of many terrestrial ecosystems, but rising global temperatures are changing snow regimes and driving widespread declines in the depth and duration of snow cover. Loss of the insulating snow layer will fundamentally change the environment – far more than incremental temperature increases. Understanding how individuals, populations, and communities respond to different snow conditions is thus essential for predicting and managing future ecosystem change. We conducted a systematic review to synthesize 365 studies that have examined ecological responses to variation in winter snow conditions. This substantial body of research encompasses a broad range of research methods (experimental manipulations, natural snow gradients, and long-term monitoring approaches), locations (35 countries), study organisms (plants, mammals, arthropods, birds, fish, lichen, and fungi), and response measures. Although we found trends towards advanced phenology with earlier snowmelt and greater mortality and/or physical injury with shallower snow, the mechanisms behind these responses remain largely unknown. With 96% of studies from the northern hemisphere, the generality of these trends across ecosystems is also unclear. We identified substantial research gaps and highlight five key areas for future research to better understand the mechanisms underlying responses to changing snow conditions and the consequences of those responses for seasonally snow-covered ecosystems.

Introduction

The presence of seasonal snow, covering the ground for weeks to months each year, is a feature of many temperate and montane ecosystems with up to a third of the Earth’s terrestrial surface covered by seasonal snow at any time (Vaughan et al. 2013). Snow is one of the most important factors governing the ecology of these ecosystems due to its influence on the timing and length of the growing season, local and regional hydrology, and soil nutrient influxes (Billings & Mooney 1968; Körner 2003; Vavrus 2007; Blankinship & Hart 2012). Yet snow conditions are changing in many parts of the world, altering winter and growing season conditions for both plants and animals and with the potential to drive significant biodiversity loss (Vaughan et al. 2013; Niittynen et al. 2018).

Mean global temperatures have increased by 0.7°C over the last 50 years (Stocker et al. 2013), with global snow cover decreasing by 10% over the same period (Walther et al. 2002). The most rapid and consistent losses of snow, in terms of both depth and duration, are mid-elevation areas (e.g. sub-alpine zone) and those with Mediterranean/maritime climates (e.g. Australian alpine region), where mean air temperatures are close to freezing and snow is primarily temperature-limited (Brown & Mote 2009; Steger et al. 2013; Vaughan et al. 2013). While shifts in regional and global atmospheric circulation patterns are driving elevated snowfall in areas where snow is limited by precipitation (e.g. high northern latitudes), these regions are still likely to experience reduced spring snow and a shorter growing season over the next 50 years (Räisänen 2008; Brown & Mote 2009; Vaughan et al. 2013).

Changes in winter precipitation and temperature regimes in seasonally snow-covered environments are mediated by the snowpack – the layer of accumulated snow – and changes to the snowpack will have diverse ecological effects (Geiger et al. 1995; Fig. 1). Experimental field manipulations that artificially advance snowmelt consistently induce earlier phenology in plants

(Wipf & Rixen 2010). With earlier spring snowmelt forecast to be among the most prominent effects of global warming on seasonal snowpacks (Déry & Brown 2007; Räisänen 2008), an overall advancement in spring phenology is expected. How organisms adapted to a seasonally snow-covered environment will respond to changes in snow conditions more generally – including the extent of cover, depth, density, and the timing of snowmelt – is, however, unclear.

The extent of snow cover determines the availability of snow-associated habitat. Both mammals and arthropods, can be active on the snow surface during winter. Small arthropods such as springtails and mites can also inhabit the snowpack itself, moving through air pockets between ice crystals and using thermal gradients within the snowpack to regulate their microclimate (Leinaas 1981; Hågvar 2010). Finally, a narrow space between the ground and the base of the snowpack – the subnivean space, or subnivium (Pauli et al. 2013) – provides a physically sheltered and thermally stable overwinter refuge for plants and animals (both active and hibernating/diapausing) (Pauli et al. 2013). Changes to the extent of snow cover will have a direct impact on the availability of these habitats (Fig. 1).

Snow depth and density determine the degree of thermal insulation offered by the snowpack (Pruitt 1970). Snow has a low thermal conductivity and, depending on density, 20 cm of snow is generally sufficient to effectively insulate the subnivean space from diel fluctuations in ambient air temperature (Pruitt 1970). This buffering effect means that subnivean organisms are expected to experience the coldest temperatures during early autumn and late spring – not during winter – in contrast to ecosystems without seasonal snow cover. Groffman et al. (2001) suggested that seasonally snow-covered ecosystems might thus experience “colder soils in a warmer world”, with snowpack decline exposing soils and organisms to air temperatures up to 15°C colder than those in a snow-buffered airspace (Mölders & Walsh 2004). A shallower snowpack will also increase ground temperature fluctuations, which are thus more likely to cross critical physiological thresholds for subnivean organisms (Geiser & Broome 1993; Marshall & Sinclair 2012; Williams et al. 2015).

The duration of snow cover directly determines growing season length for plants, with little growth and development under the snow (Körner 2003). While a longer growing season could increase productivity (e.g. Billings & Bliss 1959), snowmelt timing determines the conditions to which plants are exposed when they emerge from snow, and earlier snowmelt can increase exposure to damaging frost and extreme temperatures (Steltzer et al. 2009; Gezon et al. 2016). The timing of snowmelt influences water availability during the growing season, which is gradually released from melting snow, and late-season moisture limitation is a risk from an early snowmelt (Litaor et al. 2008; Berdanier & Klein 2011). Changes to snowmelt timing are particularly relevant for plants because they are unable to track the presence (or absence) of the snowpack, and for interactions between plants and other organisms such as pollinators and herbivores (e.g. Forrest & Thomson 2011).

The ecological responses of organisms to changes in snow conditions can be measured using both experimental and observational approaches. Experimental methods that manipulate specific aspects of the snowpack (e.g. snow depth) allow a targeted assessment of biotic responses but are often (necessarily) limited in spatial scale. Observational approaches include both natural snow gradients and multi-year monitoring. Snow gradients typically describe long-term responses of populations, species, and communities to spatial variation in snow conditions (e.g. adaptive differences in cold tolerance among populations: Briceño et al. 2014). By contrast, studies that monitor ecological responses across years with varying snow conditions generally describe shorter-term effects (e.g. body mass following years with low/high snow: Hendrichsen & Tyler 2014). Experimental, gradient, and monitoring methods provide complementary approaches for examining ecological responses to changes in snow conditions but are not often considered together.

In this review, we synthesize studies that have explored ecological responses to spatial and temporal variation in snow conditions using a systematic review approach (Pullin & Stewart 2006; Lortie 2014; Pickering & Byrne 2014). In particular, we explore (a) the geographic locations of research, (b) what has been measured and how, (c) whether any conclusions can be made about general responses to snow conditions, and (d) gaps in current knowledge and future research directions.

Methods

Search procedure and inclusion criteria

The systematic review approach provides reproducible protocols and transparent reporting for searching, screening, and extracting data from the literature to give an overview of a field (Koricheva & Gurevitch 2013; Lortie 2014). We used the Preferred Reporting Items in Systematic Reviews and Meta-Analyses (PRISMA) framework (Moher et al. 2009) to compile a database of studies that measured ecological responses to variation in snow conditions.

To identify relevant literature, we searched three databases with the term “snow” in combination with any one of the following: “manipulation”, “experimental warming”, “climate change”, “ecology”, “long-term monitoring”, “long term monitoring”, “ploughing”, “gradient”, “grooming”, “snowpatch”, “phenology”, “winter warming”, (“winter” and “climate change”). These terms were used within “Topic” in the Web of Science database, within “Abstract, title, author, keywords” in the Scopus database, and within “Keywords” in the Science Direct database, limiting results to studies in English-language journals. These searches were initially conducted in May 2016 and repeated in May 2019 to update the database, which produced 9,047 unique results (Fig. 2). To supplement this topic-based search, 24 reviews on related topics were identified that have been published since 1999 (Appendix S1). All studies citing or cited by these reviews were retrieved in May 2016, returning an additional 860 unique studies (Fig. 2). Unpublished data and "grey" literature, such as protected area management plans, were not included as much of this literature is not publicly available and is challenging to search systematically via electronic databases (Côté et al. 2013).

All studies were screened for eligibility, based on the following criteria: (1) the study was original research, not a review, and published in an English-language academic journal; (2) the study was carried out at a site where there is seasonal snow cover; (3) the study measured some form of biotic response; (4) the study measured responses to changes in snow cover. For criterion 2, we excluded studies from polar regions and permanently snow-covered areas. Cooper (2014) reviewed the effects of winter climate change on arctic ecosystems and the effects of snow regime change in permanently snow-covered ecosystems are likely to differ from those in seasonal environments, where plants and animals are adapted to snow for only part of the year. For criterion 3, we considered any form of response measured in an animal or plant but excluded studies on soil microbes. For criterion 4, we included studies that experimentally manipulated snow cover in the field ("manipulation"), those that measured responses along a snowmelt gradient ("gradient"), and those that recorded responses over multiple years across which snow conditions differed ("monitoring"). Several experimental methods can be used to reduce snow cover, including manual snow removal (e.g. Bombonato & Gerdol 2012), external heating (e.g. Adler et al. 2007), soil heating (e.g. Bokhorst et al. 2012), the addition of material that increases albedo and facilitates snowmelt (e.g. Steltzer et al. 2009), and physical covering to prevent snow accumulation (e.g. Drescher & Thomas 2013). Natural snowmelt gradients and long-term studies offer a complementary field-based approach to assess the effects of snow depth, duration, and structure on organisms. In contrast to experimental snow removal, which is limited in scale, these studies allow assessments of larger-scale and longer-term effects of growing season duration and winter snow conditions on community composition, individual behaviors, and functional traits. Studies were only included if they measured snow cover directly. A total of 365 studies met all inclusion criteria (Fig. 2; Appendix S2).

Data extraction

For each study, the following information was extracted: (1) the location (hemisphere, continent, country(ies), and study site(s)); (2) the focal taxonomic group(s); (3) the methodology, including the type of study, length of study and, for experimental studies, the form of manipulation; and (4) the type of measures made, including when responses were recorded, whether they were recorded for individuals, populations, or communities, and the type of response recorded (e.g. phenology, growth, survival, behavior).

For responses recorded during winter, we additionally recorded which snow habitat (on-snow: “snow surface”, in-snow: “intranivean”, under-snow: “subnivean”) was being used by the study organism. Data were analyzed using descriptive methods to reveal patterns in the literature and identify research gaps. Note that the numbers given in the results do not always sum to the total number of studies (365) because individual studies often included results in several categories.

In addition to the data above, which were extracted directly from each paper, we determined the general snow conditions for each study (or each site when a study included multiple sites). For each study, the latitude and longitude of the study site(s) was obtained either directly from the paper or by georeferencing named locations. For studies conducted over a large geographic area, we used an approximately central point of the study area. Data on seasonal snow classification (Sturm et al. 1995; Liston & Sturm 1998) were obtained from the Atlas of the Cryosphere, at a 0.5°×0.5° spatial resolution (Maurer 2007). Sturm et al. (1995)’s seasonal snow classification defines six classes of snow (tundra, taiga, alpine, maritime, prairie, ephemeral) based on the stratigraphy, thickness, density, crystal morphology, and thermal gradient of the snowpack, and their spatial and temporal variability. Although this classification may not apply to all areas with seasonal snow (e.g. Sanecki et al. 2006a), it is a useful standard for comparisons. Snow classification was extracted for each study/site using RASTER 2.5-8 (Hijmans 2016), RGDAL 1.2-5 (Bivand et al. 2016), and SP (Pebesma & Bivand 2005) packages in the R environment for statistical computing v3.3.0 (R Core Team 2016). The ephemeral snow classification (< 2 months snow) covers large areas across the world that do not typically have seasonal snow, therefore it was not represented on the world map. Maps were plotted using GGMAP 3.0.0 (Kahle & Wickham 2013) and GGPLOT2 3.2.1 (Wickham 2016).

To summarize the main results, we tallied studies that had shown positive, negative, nil, or mixed responses to variation in snow conditions. Although such vote-counting methods are generally unsuitable as a formal statistical technique for research syntheses (Koricheva & Gurevitch 2013), they are valuable as a summary tool and highlight areas where formal meta-analysis might be warranted in the future. This approach was chosen because sample sizes were small for most response variables and many different types of response variable were measured, limiting the utility of quantitative analysis. Responses were summarized for plants, mammals, and arthropods – groups for which there were at least 20 studies. Twelve response variables were identified that were comparable across taxonomic groups. These are presented in relation to changes in snow depth and snowmelt timing (the most common aspects of snow variation measured). Summaries of results for all response variables measured across taxa are provided in Appendix S3.

Results

Time and place

There were 365 studies on ecological responses to variation in snow conditions that met all inclusion criteria. These studies were published between 1959 and 2019 with a median study duration of 2 years (range 1 – 60 years). While studies have been conducted in 35 countries, most of the research was from the USA (118 studies, 32%), Sweden (41 studies, 11%) and Canada (33 studies, 9%), and nearly all (349, 96%) from the northern hemisphere (Fig. 3, Table 1). Studies were conducted in alpine/montane (218 studies), temperate forest or grassland (94 studies), and sub-arctic environments (112 studies) (Table 1). Two locations featured prominently: Abisko in northern Sweden (27 studies) and the Rocky Mountain Biological Laboratory in Colorado, USA (20 studies).

The study sites cover a variety of snow conditions and, in the northern hemisphere, all snow types were represented: maritime (n = 193 studies/sites), alpine (n = 86), prairie (n = 63), tundra (n = 79), and taiga (n = 31), with 38 studies lacking a snow classification. Note that a single study could have multiple sites. The predominance of studies on alpine (cold, deep snow cover) and maritime snow (warm, deep snow cover) does not correspond to the relative frequencies of these two snow types across the landscape: each are <10% of snow-covered land area in the northern hemisphere. In the southern hemisphere, maritime snow was the only snow type represented, although there were 15 sites that lacked a snow classification. This is likely due to the snow classification system being developed for northern hemisphere snow conditions, which are different to those in the southern hemisphere (Sanecki et al. 2006a).

Organisms

The impacts of seasonal snow cover have been assessed, in some way, for a broad range of plant and animal groups (Table 1). For plants (66% of all studies), this includes research on small vascular plants ($n = 158$), shrubs ($n = 72$), trees ($n = 40$), and bryophytes ($n = 21$). For animals, most of the research has focused on mammals ($n = 76$) or arthropods ($n = 23$), with few studies for birds ($n = 16$), fish ($n = 2$), reptiles ($n = 1$), or amphibians ($n = 1$). Finally, a few studies included lichens ($n = 13$) or fungi ($n = 7$). Considering only the southern hemisphere, however, there was only one study of arthropods, four studies of mammals, and 13 studies of plants.

Study approach

Research on ecological responses to variation in snow conditions has used experimental ($n = 164$) and observational ($n = 212$) methods (Table 2). This is true for research in both hemispheres, and all climatic zones. Observational studies included research using natural snow cover or snowmelt gradients ($n = 119$) and year-to-year variation in snow conditions ($n = 113$). A few studies used multiple methods: experimental manipulations with measures across snowmelt gradients ($n = 7$) or through time ($n = 5$), or long-term monitoring across snowmelt gradients ($n = 20$).

Experimental manipulations of snow depth tested the effects of both more snow (increased depth: $n = 62$; increased persistence: $n = 47$), less snow (decreased depth: $n = 68$; decreased persistence: $n = 46$), and the effects of unusual weather events (e.g. mid-winter snowmelt: $n = 14$). However, more than half of the studies that altered snow depth also altered snowmelt timing (and *vice versa*), meaning that these effects are frequently confounded. Studies that altered snow duration almost always did so by manipulating the timing of spring snowmelt, with only three studies changing the timing of snow accumulation. Experimental manipulations of the effects of snow density ($n = 17$) and snow chemistry ($n = 4$) were most often related to anthropogenic use of snow: compaction from oversnow vehicles or skiing, and changes to chemistry or density due to artificial snowmaking.

Experimental approaches were common in physiological studies, community composition, chemistry, and overwinter survival, as well as the response of arthropods (*n* = 31) and plants (*n* = 84). By contrast, gradient and monitoring studies provide most of the evidence for effects of snow conditions on animal movements (*n* = 28 and *n* = 18, respectively) and plant phenology (*n* = 33 and *n* = 44, respectively).

Timing of measurement

Experimental studies nearly always measured responses in the subsequent growing season (93% of studies), while 20% of monitoring studies and 24% of gradient studies included winter measurements (Table 2). In contrast to all other taxa, more studies measured mammal responses during winter (*n* = 49) than during the subsequent snow-free period (*n* = 32), with these studies primarily exploring activity (e.g. home range size, habitat use) in relation to snow characteristics. There were 154 studies that measured the responses of small vascular plants during the growing season, but only five (Bell & Bliss 1979; Blume-Werry et al. 2016; Saarinen et al. 2016; Tessier 2017; Mo et al. 2018) included measurements of winter response. In total, only 71 (19%) studies, of which only 22 were studies on non-mammalian organisms, included winter measurements.

Ecological responses to snow variation

We recorded 214 different response variables measured, across all studies (Appendix S3). Taking 12 response variables that are comparable to some extent between plants, mammals, and arthropods (Fig. 4), three results stand out. First, earlier snowmelt was consistently associated with earlier spring phenology across all groups (Fig. 4). Second, reduced snow depth was frequently associated with higher mortality and/or damage in plants; this effect was not clear for either arthropods or mammals, nor was there a clear association with snowmelt timing. Third, there seemed to be no clear directional effect of changes in either snow depth or snowmelt timing on body size (for animals) or total biomass (for plants), or on abundance/relative cover overall

(Appendix S3). In addition, variation in snow conditions was often (37 of 49 studies) associated with differences in plant and arthropod community composition in experimental, gradient, and monitoring studies.

Discussion

There is a substantial body of research on ecological responses to changes in snow conditions, ranging from studies of habitat use by large mammals during winter, to those testing the effects of shallow snow cover on plant physiology. These studies encompass many locations, study organisms, research methods and response variables, reflecting the widespread ecological importance of snow. Nevertheless, the large number of studies belies a thin research coverage for many taxa, locations, and research questions, and there are several notable gaps in the current literature, including geographic gaps and the measurement of winter responses.

Research on seasonal snow cover is geographically skewed

Snow occurs on every continent, but this is only partly reflected in the locations of research on seasonal snow, which is strongly biased towards European and North American mountain systems. Notably absent were studies from South America, Africa, and the sub-Antarctic. The Andes range in South America maintains both permanent and seasonal snowpacks, with the latter covering approximately 61,000 km^2 and accounting for 98% of snow-covered area on the continent (Saavedra et al. 2017). In the Chilean Andes, Cavieres and Arroyo (2000) found that seeds of the herb *Phacelia secunda* from higher elevations needed longer periods of cold prior to germination than those from lower elevation populations, however this study did not specifically examine effects of snow conditions. In Africa there are mountain systems with seasonal snow, including the Atlas Mountains in Algeria, Morocco and Tunisia, mountains in the Eastern Cape region of South Africa, and the Maluti Mountains in Lesotho. Studies from low-elevation forest and grassland, many of which have “prairie”, “tundra” or “taiga” snow types, were also globally scarce, perhaps reflecting relatively higher human land-use across these areas.

Large regional differences in snow regimes, the drivers of snow cover variation (e.g. temperature- *vs* precipitation-limitation), and the likely impacts of climate change on snow conditions (Räisänen 2008) mean that expanding studies to include these underrepresented areas is important. The type and nature of the biota present also differs among regions and ecosystems (e.g. Sinclair & Chown 2005; Bannister 2007). In Australia, for example, snow-covered environments have many scleromorphic shrubs and no large mammals (Green & Osborne 2012). This ecosystem is likely to have fundamentally different responses to changes in snow conditions compared to, for example, a northern boreal forest with many large mammals.

While the ecological effects of snow might vary geographically due to differences in the underlying nature of the biota, variation might also be driven by differences in effects of changing snow conditions on the abiotic environment. When mean ambient air temperatures are above freezing, loss of the insulating snowpack should tend to increase, rather than decrease near-ground temperatures (Slatyer et al. 2017). By contrast, ambient winter air temperatures are well below freezing in many seasonally snow-covered ecosystems, driving a decrease in near-ground temperature with a reduced snowpack (e.g. Groffman et al. 2001; Decker et al. 2003; Tan et al. 2014; Petty et al. 2015). If the physical effects of reduced snow cover vary among regions, then inferences regarding ecological impacts will necessarily be region-specific. It is thus critical that studies of snow ecology measure and consider these differences. Conducting further studies in seasonally snow-covered areas of the southern hemisphere and other regions where the abiotic and/or ecological effects of reduced snow might be unique is essential to better understand which ecological impacts could be generalizable and which are specific to particular regions or snow conditions.

Winter responses: the black box

Fifteen years since Campbell et al. (2005) highlighted a paucity of ecological studies during winter, measurements of winter responses to variable snow conditions remain limited. Only 71 of the 365 studies included in this review measured responses during the winter. Two studies of arthropods exemplify the value in measuring winter responses: following experimentally reduced snow cover, abundances of small arthropods were lower during the winter but, at the scale of the experiment, these effects did not carry over into the growing season (Sulkava & Huhta 2003; Bokhorst et al. 2013). For grazing mammals such as the Svalbard reindeer, climate warming has potential to lead to opposing effects on body mass in summer and winter. While warming during the growing season might increase plant growth and forage availability, winter warming that increases rain-on-snow events that in turn cause icing will restrict winter grazing, thereby reducing body mass (Albon et al. 2017). In these examples, measurements made only during the growing season would have failed to detect or explain the effects of changing snow conditions.

Among the studies included here, most of the winter measurements were on habitat use and activity patterns of mammals moving on the snow surface, with a tendency for individuals to favor areas with shallower snow than surrounding habitat (e.g. Mermod & Liberek 2002; Kolbe et al. 2007; Matthews 2010). An additional three studies examined how snow conditions affected habitat use and overwinter survival for subnivean animals. Artificially expanding the subnivean space increased winter activity and improved the overwinter survival of voles in Norway (Korslund & Steen 2006), while reducing the subnivean space lowered detection of small mammals in Australia (Sanecki et al. 2006b). However, winter survival of bank voles was not related to subnivean temperature or snow depth (Johnsen et al. 2018), with food availability more important than subnivean habitat structure for abundance and overwinter survival (Johnsen et al. 2017). Shallow snow, and the associated increase in temperature fluctuations, can also increase the energy expenditure of hibernating subnivean mammals and dormant arthropods (e.g. Geiser

& Broome 1993; Irwin & Lee 2003). Taken together, these studies suggest contrasting effects of reduced snow on snow-surface and subnivean fauna.

The ecology of the subnivean environment remains elusive. With the exception of a detailed series of studies in Canada (e.g. Aitchison 1979a, b, c, 1984) and a couple of others (Berzitis et al. 2017; Slatyer et al. 2017), there are few surveys of subnivean arthropods and, although many mammals, reptiles, and amphibians are known or assumed to overwinter beneath the snow, their winter ecology is generally not well known. A second ecological unknown is the snow layer itself. Despite extensive searching of the literature, we found no studies that examined how changes in snow conditions might affect the intranivean fauna – small arthropods such as mites and springtails living within the snow layer itself. One might expect these organisms to be affected by the depth, density, and/or crystal structure of the snowpack, which affect the temperature gradient within the snowpack and the size of the spaces through which animals can move (Marchand 2013). While Leinaas (1981) studied movements of intranivean arthropods within the snowpack and (Hågvar 2010) provided an overview of intranivean taxa, we are unaware of further work on this topic.

Conclusions

The results of our systematic review provide a tantalizing glimpse into possible effects of snow conditions on organisms during winter, with individual studies showing that physiology, patterns of activity, habitat use, and foraging behavior can each be influenced by snow conditions. Winter-time frost hardiness, for example, has been shown to be greater for shrubs under deeper snow in both experimental (Taulavuori et al. 2011) and gradient studies (Palacio et al. 2015). These results hint at both short-term (plastic) and long-term (adaptive) physiological adjustments to variation in snow conditions. How such effects translate into growing season responses remains unclear, but linking winter and growing season effects (e.g. Korslund & Steen 2006) will be an important avenue for future research.

By evaluating the current literature on ecological effects of changing snow conditions in seasonally snow-covered environments, this review provides an outline of where, how, and what research has been published, highlighting several knowledge gaps. Although many studies have examined ecological effects of changes in seasonal snow, when studies are divided by taxonomic group, location or climate zone, these numbers rapidly attenuate. There is ample scope for future research that both broadens the current literature and adds depth and detail to what already exists.

We highlight five key areas for future research:

1. Additional studies in underrepresented snow-covered areas, including the Andes mountain range in South America, the southern hemisphere generally, and low-elevation grassland and forest. These studies should be accompanied by measures of microclimate, so that observed ecological responses can be compared with studies from other regions.
2. Integration of natural snowmelt gradients with experimental manipulations or long-term monitoring (e.g. Dunne et al. 2004; Cornelius et al. 2013). Understanding how changing snow conditions will affect species and communities adapted to different snow conditions will require integrated approaches. Variation in, for example, physiological tolerances (e.g. Vrba 2012; Briceño et al. 2014), developmental temperatures (e.g. Forrest & Thomson 2011), or species interactions (e.g. Callaway et al. 2002) in areas with naturally high or low snow cover could affect responses to changing snow conditions.
3. Exploring the effects of changing snow conditions on species interactions. Only 14 of the studies in this review explicitly tested species interactions (but see also Nystuen et al. 2014; Penczykowski et al. 2017). Early snowmelt could have large impacts on plant-

pollinator and plant-herbivore interactions by generating phenological mismatches (e.g. Kudo & Ida 2013).

4. Investigations into the mechanisms underlying higher mortality/injury with reduced snow/early snowmelt for plants. For example, is mortality caused by an accumulation of sub-lethal injuries or a single extreme event? Injury could similarly be caused by many factors such as species interactions (e.g. herbivory: Roy et al. 2004; fungal attack: Graae et al. 2008), physical damage from ice formation (e.g. Briceño et al. 2014), and physiological stress (e.g. Bokhorst et al. 2010). While similar mechanisms might be expected to affect mortality/injury in arthropods (e.g. ice encasement: Coulson et al. 2000; food availability: Konestabo et al. 2007; crossing physiological thresholds: Marshall & Sinclair 2012), further studies testing both responses to changing snow conditions and the mechanisms behind these are needed.
5. Tests of the effects of early snowmelt on recruitment (e.g. seed germination and seedling establishment in plants Milbau et al. 2013; and hatching success in arthropods). Phenological shifts induced by early snowmelt are likely to cause decoupling between life stage and the climatic conditions to which that life stage has historically been exposed. Effects on recruitment, which typically manifest early in the growing season, will potentially have larger impacts at the ecosystem level than effects on adult growth.

Seasonal snow is a central feature in the ecology of many terrestrial ecosystems. With continued climate change altering snow regimes worldwide, an understanding of how individuals, populations, species, and communities respond to different snow conditions is essential for predicting and managing future ecosystem change. There is great scope for more research on ecological effects of snow, both in terms of geographic and taxonomic breadth, and uncovering the most salient effects that might themselves be region- or species-specific.

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Supporting Information

Appendix S1. Summary of studies identified via review searches.

Appendix S2. Citation details for all studies included in the review.

Appendix S3. Summary tables of responses of plants, mammals, and arthropods to reduced snow conditions.

Data availability

The full database of studies included in the review is available at: 10.6084/m9.figshare.4977998

Tables

Table 1. Summary of location and study organism information for original research papers examining ecological effects of snow conditions. Percentages given are out of the total number of studies (365) and do not always add up to 100 as some studies covered multiple categories.

Category	**Total**		**Category**	**Total**
All papers	365			
Continent/region			**Taxonomic/functional group**	
Europe	159 (44%)		Plant	241 (66%)
North America	149 (41%)		Small vascular plant	158 (43%)
Asia	40 (11%)		Shrub	72 (20%)
Australia	12 (3%)		Tree	40 (11%)
Oceania	6 (2%)		Bryophyte	21 (6%)
South America	0 (0%)		Animal	131 (36%)
Africa	0 (0%)		Mammal	76 (21%)
			Arthropod	37 (10%)
Climate zone			Bird	16 (4%)
Temperate alpine	157 (43%)		Fish	2 (1%)
Sub-arctic/boreal	112 (31%)		Reptile	1 (< 1%)
Temperate sub-alpine	61 (17%)		Amphibian	1 (< 1%)
Temperate forest	57 (16%)		Lichen	13 (4%)
Temperate grassland	37 (10%)		Fungi	7 (2%)
Sub-Antarctic	0 (0%)			
Tropical alpine	0 (0%)			

Table 2. Summary of methodological approaches used to study the ecological effects of snow conditions on plants and animals. Percentages given are out of the total number of studies (365) and do not always add up to 100 because some studies covered multiple categories.

Category	Total
Type of study	
Experimental	164 (45%)
Snow depth	114 (31%)
Snow duration	75 (21%)
Snow density	20 (5%)
Snow chemistry	4 (1%)
Observational	212 (58%)
Spatial variation	119 (33%)
Temporal variation	113 (31%)
Timing of measurement	
Summer	309 (85%)
Winter	71 (19%)
Snow-surface	59 (16%)
Intranivean	0 (0%)
Subnivean	17 (5%)

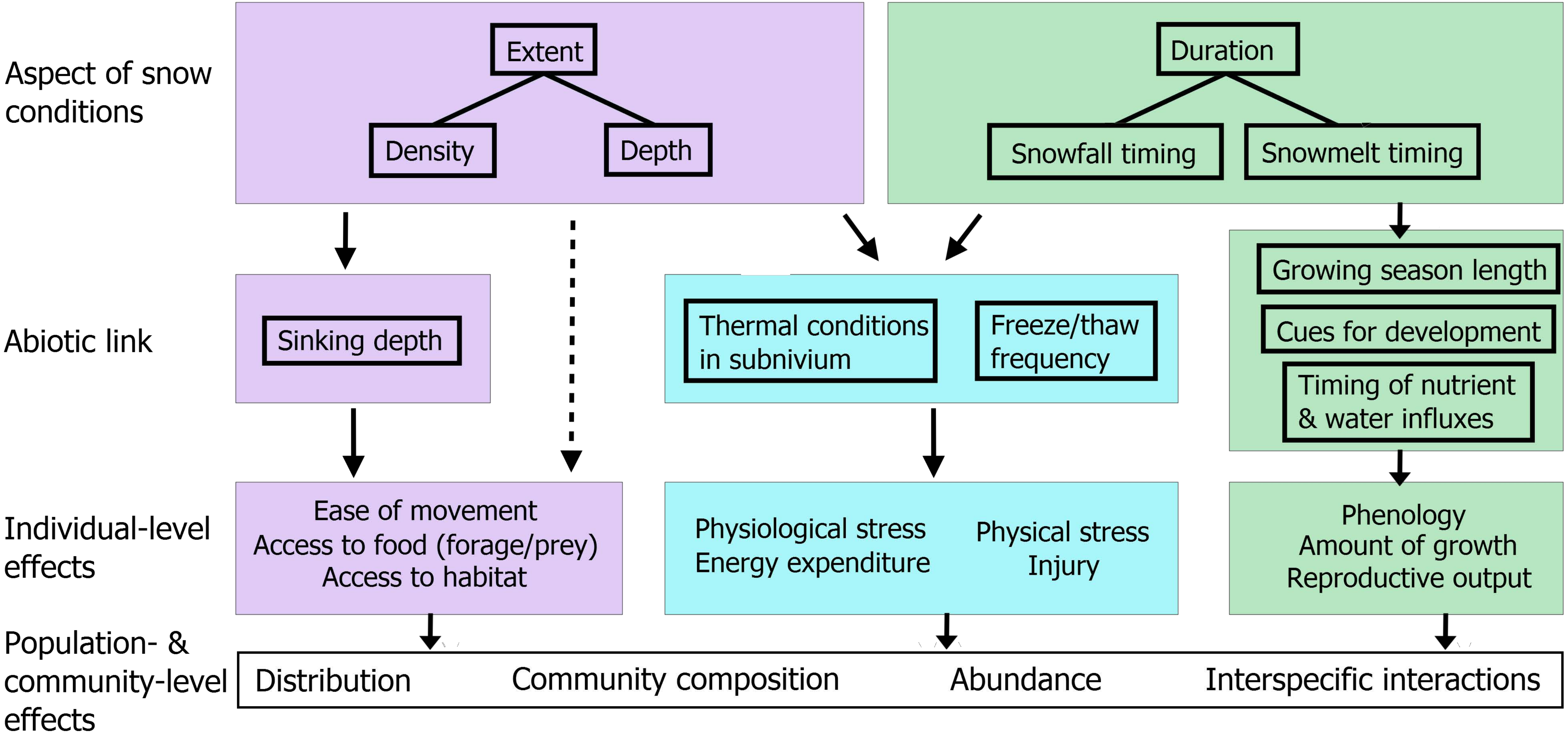
Figure legends

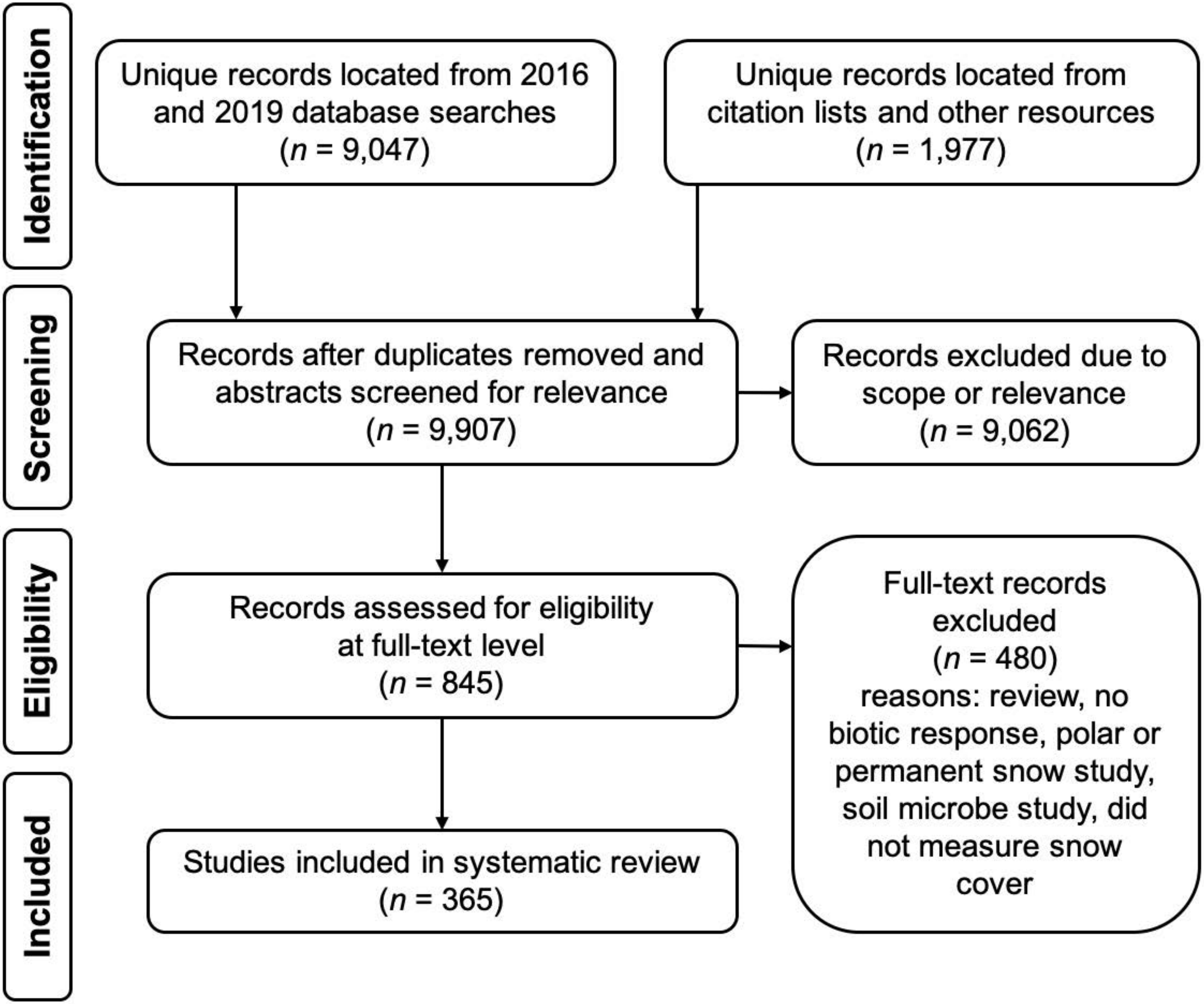
Figure 1. Some potential effects of changing snow conditions on organisms in seasonally snow-covered environments. Different colors are indicative of the type of effect (e.g. behavior, physiology, growth) that the change in snow condition might have.

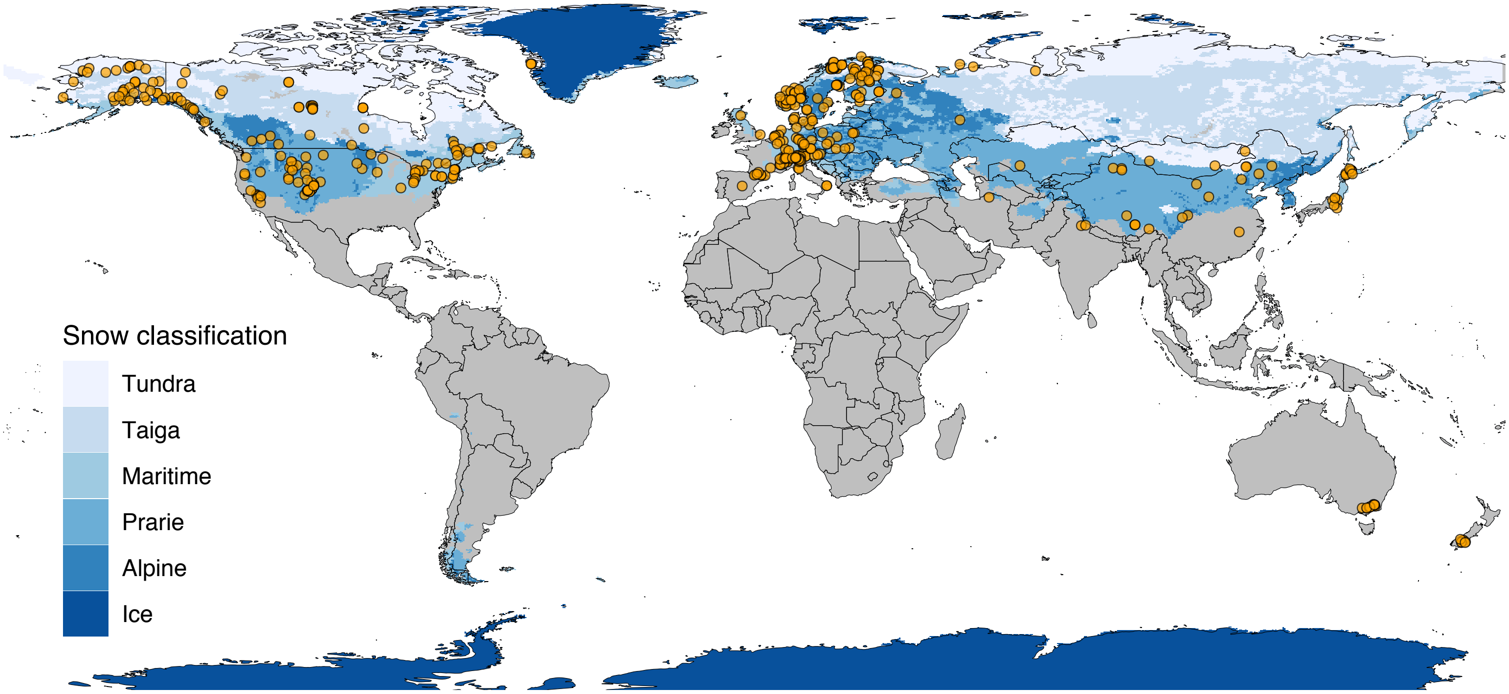
Figure 2. Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA: Moher et al. 2009) flowchart, outlining the process followed to compile the dataset used in the literature review; *n* = number of original research papers (studies).

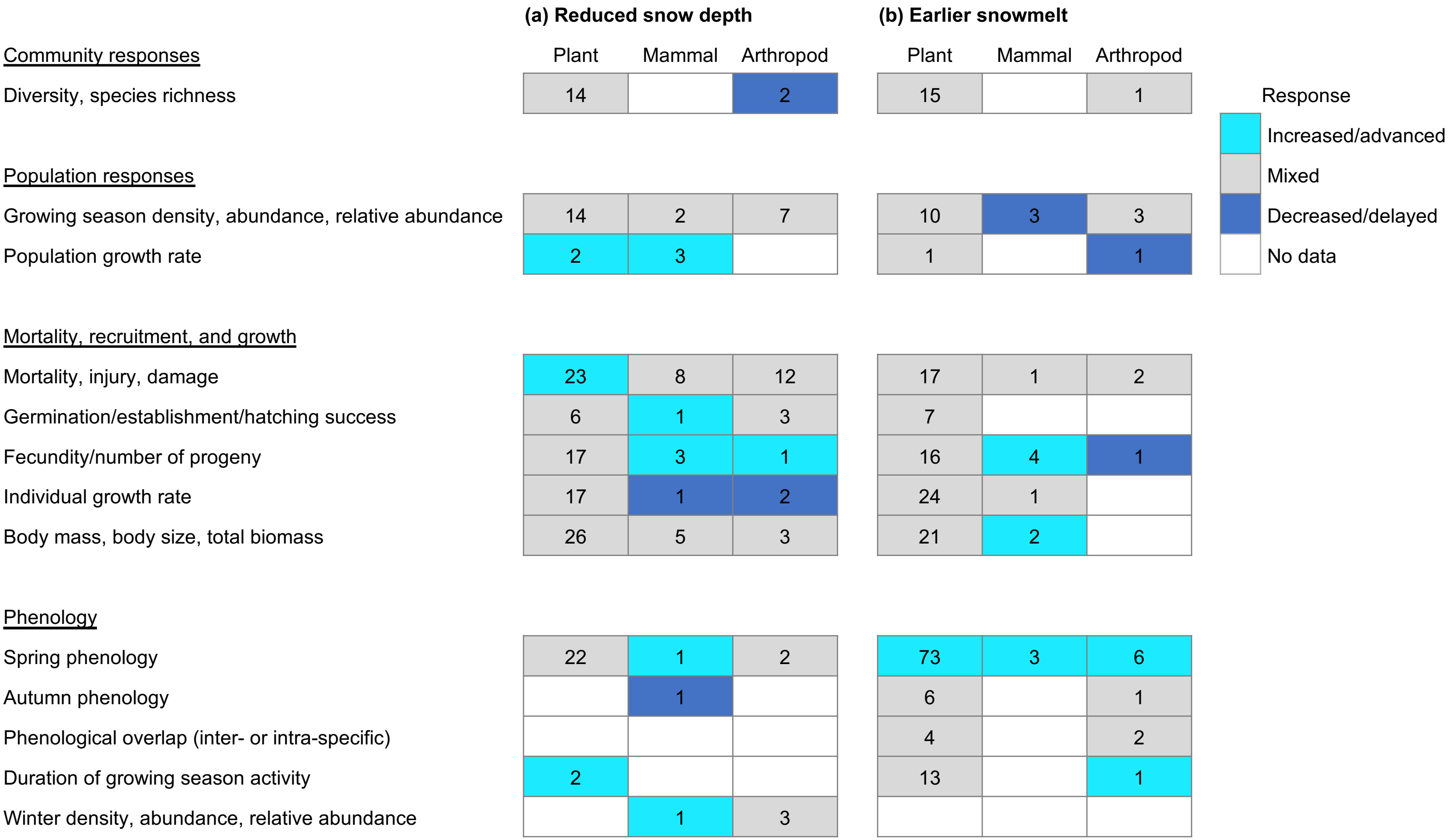
Figure 3. Distribution of study sites in relation to snow type and geography. Colors indicate different snow classifications according to Sturm et al. (1995) and studies included in the review are shown as orange circles. Snow classification data were obtained from the Atlas of the Cryosphere (Maurer 2007). Note some regions with seasonal snow, primarily in the southern hemisphere, do not have a classification according to the system of Sturm et al. (1995).

Figure 4. Summary of responses of plants, mammals, and arthropods to changes in snow depth and the timing of snowmelt, based on a simple vote-counting procedure (see Methods). Response variables are on the left and responses are shown in relation to (a) reduced snow depth and (b) earlier snowmelt; numbers indicate the number of studies. Light blue shading indicates a higher value or an earlier occurrence (for autumn/spring phenology) in > 50% of studies; dark blue shading indicates a lower value or a later occurrence in > 50% of studies. Grey shading indicates no clear directional response; this could be due to different studies showing results in opposite directions, individual studies showing mixed results, or individual studies showing no effect of snow variation on the response variable. Unfilled boxes indicate no studies.


Aspect of snow conditions
Extent
Density
Depth
Duration
Snowfall timing
Snowmelt timing
Abiotic link
Sinking depth
Thermal conditions in subnivium
Freeze/thaw frequency
Growing season length
Cues for development
Timing of nutrient & water influxes
Individual-level effects
Ease of movement
Access to food (forage/prey)
Access to habitat
Physiological stress
Energy expenditure
Physical stress
Injury
Phenology
Amount of growth
Reproductive output
Population- & community-level effects
Distribution
Community composition
Abundance
Interspecific interactions


Identification
Screening
Eligibility
Included
Unique records located from 2016 and 2019 database searches (*n* = 9,047)
Unique records located from citation lists and other resources (*n* = 1,977)
Records after duplicates removed and abstracts screened for relevance (*n* = 9,907)
Records excluded due to scope or relevance (*n* = 9,062)
Records assessed for eligibility at full-text level (*n* = 845)
Full-text records excluded (*n* = 480) reasons: review, no biotic response, polar or permanent snow study, soil microbe study, did not measure snow cover
Studies included in systematic review (*n* = 365)


Snow classification
Tundra
Taiga
Maritime
Prarie
Alpine
Ice



	(a) Reduced snow depth			(b) Earlier snowmelt		
	Plant	Mammal	Arthropod	Plant	Mammal	Arthropod
Community responses						
Diversity, species richness	▨ 14	□	▼ 2	▨ 15	□	▨ 1
Population responses						
Growing season density, abundance, relative abundance	▨ 14	▨ 2	▨ 7	▨ 10	▼ 3	▨ 3
Population growth rate	▲ 2	▲ 3	□	▨ 1	□	▼ 1
Mortality, recruitment, and growth						
Mortality, injury, damage	▲ 23	▨ 8	▨ 12	▨ 17	▨ 1	▨ 2
Germination/establishment/hatching success	▨ 6	▲ 1	▨ 3	▨ 7	□	□
Fecundity/number of progeny	▨ 17	▲ 3	▲ 1	▨ 16	▲ 4	▼ 1
Individual growth rate	▨ 17	▼ 1	▼ 2	▨ 24	▨ 1	□
Body mass, body size, total biomass	▨ 26	▨ 5	▨ 3	▨ 21	▲ 2	□
Phenology						
Spring phenology	▨ 22	▲ 1	▨ 2	▲ 73	▲ 3	▲ 6
Autumn phenology	□	▼ 1	□	▨ 6	□	▨ 1
Phenological overlap (inter- or intra-specific)	□	□	□	▨ 4	□	▨ 2
Duration of growing season activity	▲ 2	□	□	▨ 13	□	▲ 1
Winter density, abundance, relative abundance	□	▲ 1	▨ 3	□	□	□

Response
- ▲ Increased/advanced
- ▨ Mixed
- ▼ Decreased/delayed
- □ No data