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

Rachel A. Slatyer*, Pieter A. Arnold

Division of Ecology & Evolution, Research School of Biology, The Australian National University, Canberra, ACT, Australia

* Corresponding author: Rachel A. Slatyer
Address: 46 Sullivans Creek Rd, Acton, ACT 2600, Australia
Email: rachel.slatyer@anu.edu.au

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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. Understanding how individuals, populations, and communities respond to different snow conditions is thus essential for predicting and managing future ecosystem change. We synthesized 365 studies that have examined ecological responses to variation in winter snow conditions. This research encompasses a broad range of 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. Earlier snowmelt was consistently associated with advanced spring phenology in plants, mammals, and arthropods. Reduced snow depth also often increased mortality and/or physical injury in plants, although there were few clear effects on animals. Neither snow depth nor snowmelt timing had clear or consistent directional effects on body size of animals or biomass of plants. With 96% of studies from the northern hemisphere, the generality of these trends across ecosystems and localities is also unclear. We identified substantial research gaps for several taxonomic groups and response types, with notably scarce research on winter-time responses. We have developed an agenda for future research to prioritize understanding of 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). Snow conditions are changing in many parts of the world, however, altering winter and growing season conditions for both plants and animals have the potential to drive significant biodiversity loss (Vaughan et al. 2013; Niittynen et al. 2018).

Global mean land surface temperatures have increased by 0.7°C over the last 50 years (Stocker et al. 2013), while the area of snow cover has decreased by up to 13% in mountain regions in just 18 years (Notarnicola 2020). 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). However, while some plants may respond by flowering earlier, their pollinators may respond to different phenological cues (e.g. temperature vs light) that subsequently could drive phenological mismatches between plants and pollinators, reducing seed-set success and impacting populations (Kudo & Ida 2013). Similarly, differences in phenological responses of vegetation and herbivorous mammals can extend periods without available forage and lead to starvation (Morrison et al. 2009). Other aspects of winter snow, including the extent of cover, depth, and density, can also be important factors from an ecological perspective.

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 while small arthropods such as springtails and mites can also inhabit the snowpack itself (the intranivean), moving through air pockets between ice crystals and using thermal gradients within the snowpack to regulate their microclimate (Leinaas 1981; Hågvar 2010). A narrow space between the ground and the base of the snowpack – the subnivean space – provides a third snow-associated habitat, which is a physically sheltered and thermally stable overwinter refuge for plants and animals (Pauli et al. 2013). Changes to the extent of snow cover will have a direct impact on the availability of these habitats (Fig. 1), while at the same time altering (generally expanding) the habitat area available to species whose distribution is constrained by snow.

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 (Marshall & Sinclair 2012; Williams et al. 2015a). This, in turn, is expected to impact overwinter survival and/or condition coming into spring (Geiser & Broome 1993). In the endangered mountain pygmy possum (*Burramys parvus*), for example, individuals lose almost four times more body mass per day during winter when temperatures are just 2°C colder than their normal subnivean conditions (Geiser & Broome 1993) and low abundance following years with low snow has been reported (Green & Pickering 2002).

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 and reduce recruitment (Steltzer et al. 2009; Gezon et al. 2016). Further, the timing of snowmelt influences water availability during the growing season 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 pollinators or 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 and relatively congruent approaches for examining ecological responses to changes in snow conditions but differ in the magnitude of change that they can estimate (Elmendorf et al. 2015).

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 general conclusions can be made about 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 by one to two people, 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 approach to assess the effects of snow depth, duration, and structure on organisms. 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 excluded if they used a proxy for snow conditions (e.g. elevation), rather than measuring the relevant snow variable (e.g. depth, persistence, density) directly. This is because snow conditions are heterogeneous over small spatial and temporal scales (Litaor et al. 2008) and proxy measurements can thus be unreliable. An exception was made for studies that used measurements of soil temperature to determine the timing of snow accumulation or melt, as this is a widely accepted and reliable method (Lundquist & Lott 2008). 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), 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).

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. 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 (Table 1) and results were tallied 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 studies, 96%) from the northern hemisphere (Fig. 3, Table 2). Studies were conducted in alpine/montane (218 studies), temperate forest or grassland (94 studies), and sub-arctic environments (112 studies) (Table 2). 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 (193 studies), alpine (86 studies), prairie (63 studies), tundra (79 studies), and taiga (31 studies). 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 2). For plants (66% of all studies), this includes research on small vascular plants, shrubs, trees, and bryophytes (Table 2). For animals, most snow-related research has focused on mammals or arthropods (together 86% of animal studies), with few studies for birds, fish, reptiles, or amphibians (Table 2). Finally, a few studies included lichens (13 studies) or fungi (7 studies). 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 (164 studies) and observational (212 studies) methods (Table 3). This is true for research in both hemispheres and all climatic zones. Observational studies included research using natural snow cover or snowmelt gradients (119 studies) and year-to-year variation in snow conditions (113 studies). A few studies used multiple methods: experimental manipulations with measures across snowmelt gradients (7 studies) or through time (5 studies), or long-term monitoring across snowmelt gradients (20 studies).

Experimental manipulations of snow depth tested the effects of both more snow (increased depth: 62 studies; increased persistence: 47 studies), less snow (decreased depth: 68 studies; decreased persistence: 46 studies), and the effects of unusual weather events (e.g. mid-winter snowmelt: 14 studies). 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 snow density (17 studies) and snow chemistry (4 studies) 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 commonly used to test impacts on physiology, community composition, chemistry, and overwinter survival, and for both arthropods (31 studies) and plants (84 studies). By contrast, gradient and monitoring studies provide most of the evidence for effects of snow conditions on animal movements (28 and 18 studies, respectively) and plant phenology (33 and 44 studies, 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 3). In contrast to all other taxa, more studies measured mammal responses during winter than during the subsequent snow-free period (49 and 32 studies, respectively) with these studies primarily exploring activity or behavior (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 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 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 represent 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 in geographic representation and research approach.

Research on seasonal snow cover is geographically skewed

Snow occurs on every continent, but snow research is strongly focused on European and North American mountain systems (Cavieres & Arroyo 2000). There are several reasons why the need for expansion of research into underrepresented geographic areas and snow types is pressing. First, predictions for how snow conditions will change over the coming decades vary regionally and by elevation, with marginal snow environments – those where temperatures are already close to freezing – likely to experience the first and greatest losses of snow (Steger et al. 2013). Second, the type and nature of the biota 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. Third, with snow acting as a buffer between ambient and subnivean conditions, the abiotic effects of altered snow conditions are not geographically uniform. For example, where mean ambient air temperatures are above freezing, loss of the insulating snowpack should tend to increase near-ground temperatures (Slatyer et al. 2017). By contrast, ambient winter air temperatures well below freezing in many seasonally snow-covered ecosystems drive lower near-ground temperatures when snow is shallow (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.

Our systematic review did not find a single study explicitly testing the effects of changing snow conditions on plant or animal species in South America and Africa (but see Cavieres & Arroyo 2000). Seasonally snow-covered areas represent a tiny fraction of the total land area of these continents (0.01% and 1.2%, respectively; Hammond et al. 2018) and, as a consequence, species have few options to track their climatic niches to higher elevations or latitudes. This is especially true in Africa, where snow-covered areas are fragmented and there is no permanent snowpack; it is also one of the few places in the world where seasonal snow exists in tropical latitudes (Hammond et al. 2018; Kidane et al. 2019). As such, while the lack of snow ecology research may be unsurprising, it is no less – and arguably more – important to understand the impacts of changing snow conditions on these ecosystems.

Winter responses

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. Winter measurements are crucial for uncovering the mechanisms behind growing season responses to changing snow conditions (e.g. Albon et al. 2017), yet only 71 of the 365 studies included in this review measured responses during the winter. This likely reflects the inherent practical challenges of studying life in or under the snow. Some seasonally snow-covered regions regularly receive several meters of winter snow, making it difficult – though not impossible – to even reach the intranivean or subnivean spaces (e.g. Homma 1997). From the perspective of both practicality and conservation importance, marginal snow environments should be high priorities for studying wintertime impacts of reduced snow.

To-date, winter measurements focus 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). 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), there are few surveys of subnivean arthropods (Berzitis et al. 2017; Slatyer et al. 2017) and, although many mammals, reptiles, and amphibians are known or assumed to overwinter beneath the snow (Pauli et al. 2013), their winter ecology is generally not well known. A second ecological unknown is the snow layer itself. 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 snowpack temperature gradient and the size of the spaces through which animals can move (Leinaas 1981; Marchand 2013).

A final point regarding winter responses concerns not the species already inhabiting seasonally snow-covered environments but those whose distribution is constrained by the presence of snow. The composition of both plant and arthropod communities consistently change with variation in snow depth and duration (see Results), a testament to the role of snow as an environmental filter. In some cases, however, easing of this filter, for instance an earlier snowmelt and hence a longer growing season, could threaten the existence of specialized communities (Williams et al. 2015b) or facilitate the spread and population growth of invasive species over and above the effects of warmer temperatures alone (Stevens & Latimer 2015). While our review has focused on species species occupying seasonally-snow covered environments, these environments are not isolated islands and further work is needed to understand the impacts of changing snow conditions.

An agenda for snow ecology research

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. Fortunately, scientific understanding of snow ecology is growing rapidly in both breadth and depth, and from this review we suggest six key areas in an agenda for future research:

1. Additional studies in underrepresented snow-covered areas, including in Africa and the Andes mountain range in South America. 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 that impact (mostly negatively) both sides of the interaction (Kudo & Ida 2013; Lameris et al. 2018).
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 stages 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 population-level than effects on adult growth.
6. Targeted research syntheses. For the most studied response variables, the effect of changing snow conditions could be examined at a species level under a meta-analytical statistical framework. This may be especially useful to quantitatively explore the drivers or moderator variables for the categories that had mixed responses.

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. 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, and, more importantly, where major knowledge gaps and research opportunities remain. 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.

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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 the twelve response variables considered to be comparable across taxonomic groups. Additional variables are included in Appendix S3.

Response group	**Response**	**Description/examples**
Community	Diversity, species richness	Any measure of species diversity, richness, or evenness in a community
Population	Growing season density, abundance, relative abundance	Population density, abundance, or relative abundance, measured during the snow-free period
	Population growth rate	Typically the population growth rate over a growing season
Mortality, recruitment, and growth	Mortality, injury, damage	Overwinter mortality, mortality over the subsequent growing season, physical injury or damage (e.g. frost damage in plants)
	Germination/establishment/hatching success	The proportion of young surviving early life stages, as relevant to the organism
	Fecundity	Number of seeds, eggs, offspring produced, as relevant to the organism
	Individual growth rate	The rate of height, weight, or biomass gain, or the time to reach successive life stages, over winter in the subsequent growing season
	Body mass, body size, biomass	Measures of individual size, as relevant to the organism
Phenology	Spring phenology	The timing of ecological events at the beginning of the growing season, including bud burst and flowering (plants), emergence (insects, mammals) and migration (mammals)
	Autumn phenology	The timing of ecological events at the end of the growing season, including the onset of dormancy (plants), the end of activity (insects), and migration (mammals)
	Phenological overlap (inter- or intra-specific)	Temporal overlap between, for example: plant flowering and pollinator arrival or activity; phenological events within plant populations or communities
	Duration of growing season activity	The length of time in which growing season activities occurred

Table 2. 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 3. 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		Category	Total
Type of study			**Timing of measurement**	
Experimental	164 (45%)		Summer	309 (85%)
Snow depth	114 (31%)		Winter	71 (19%)
Snow duration	75 (21%)		Snow-surface	59 (16%)
Snow density	20 (5%)		Intranivean	0 (0%)
Snow chemistry	4 (1%)		Subnivean	17 (5%)
Observational	212 (58%)			
Spatial variation	119 (33%)			
Temporal variation	113 (31%)			

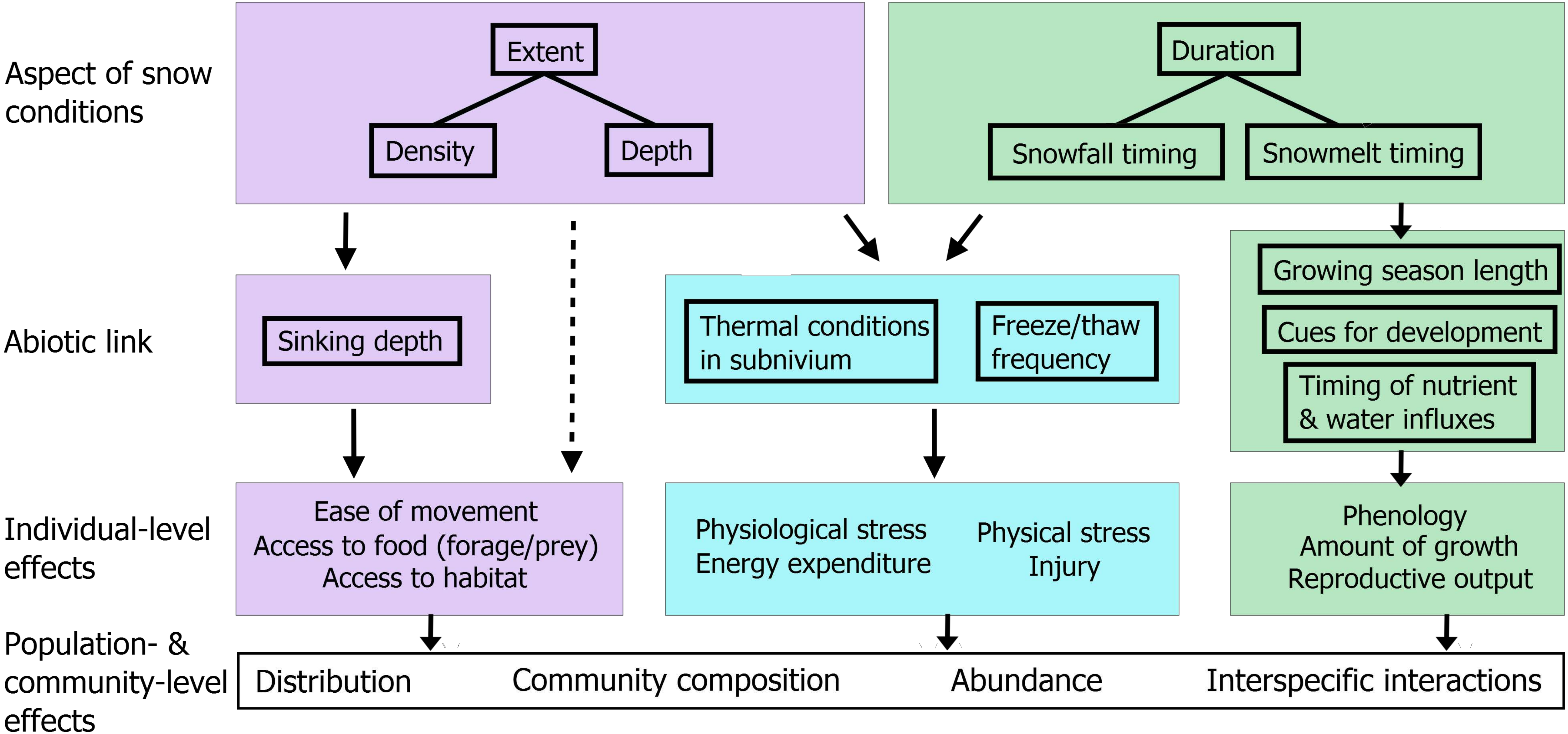
Figure legends

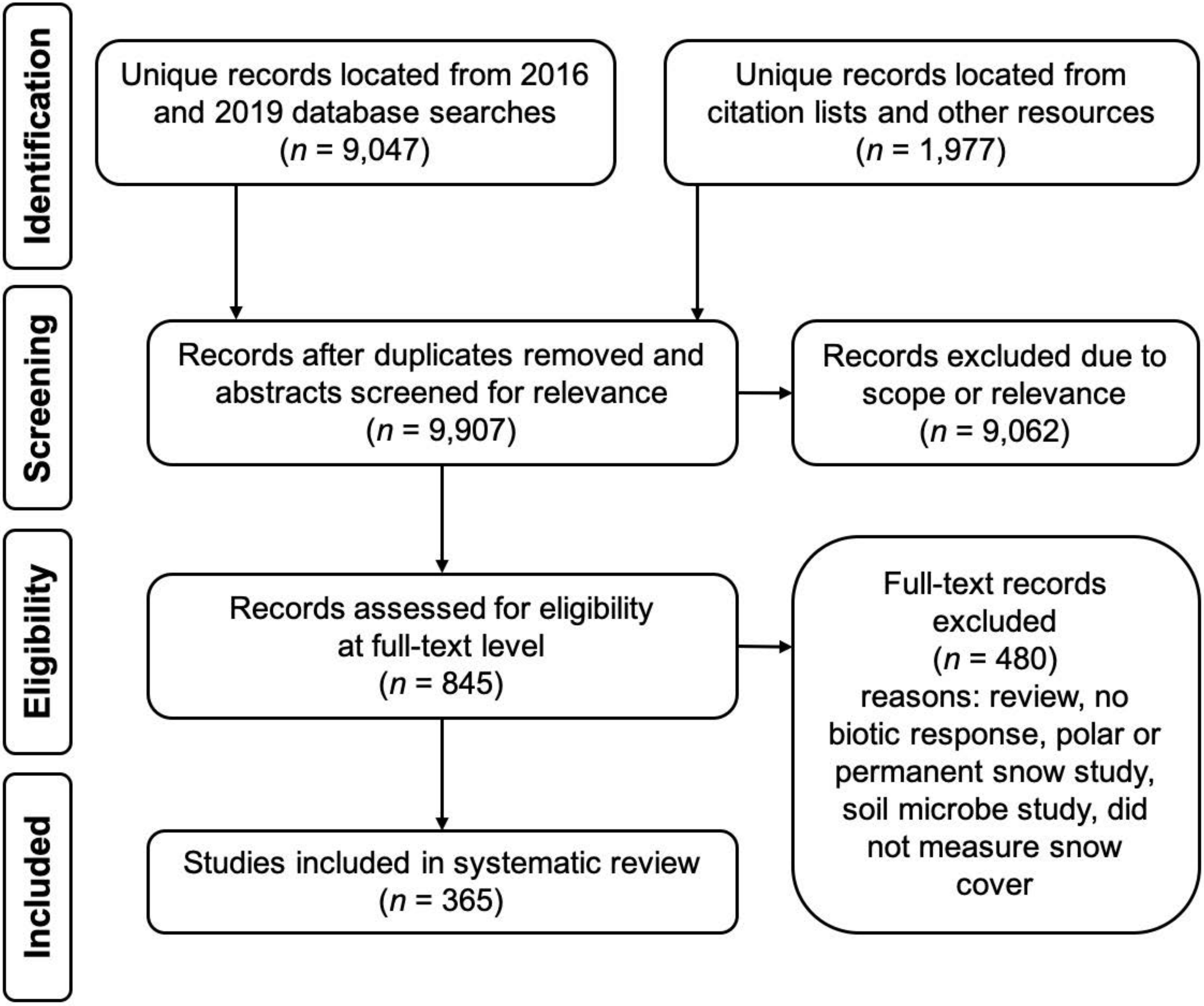
Figure 1. Some potential effects of changing snow conditions on organisms in seasonally snow-covered environments. Different colors are indicative of the type of effect (e.g. behavior, physiology, growth) that the change in snow condition might have.

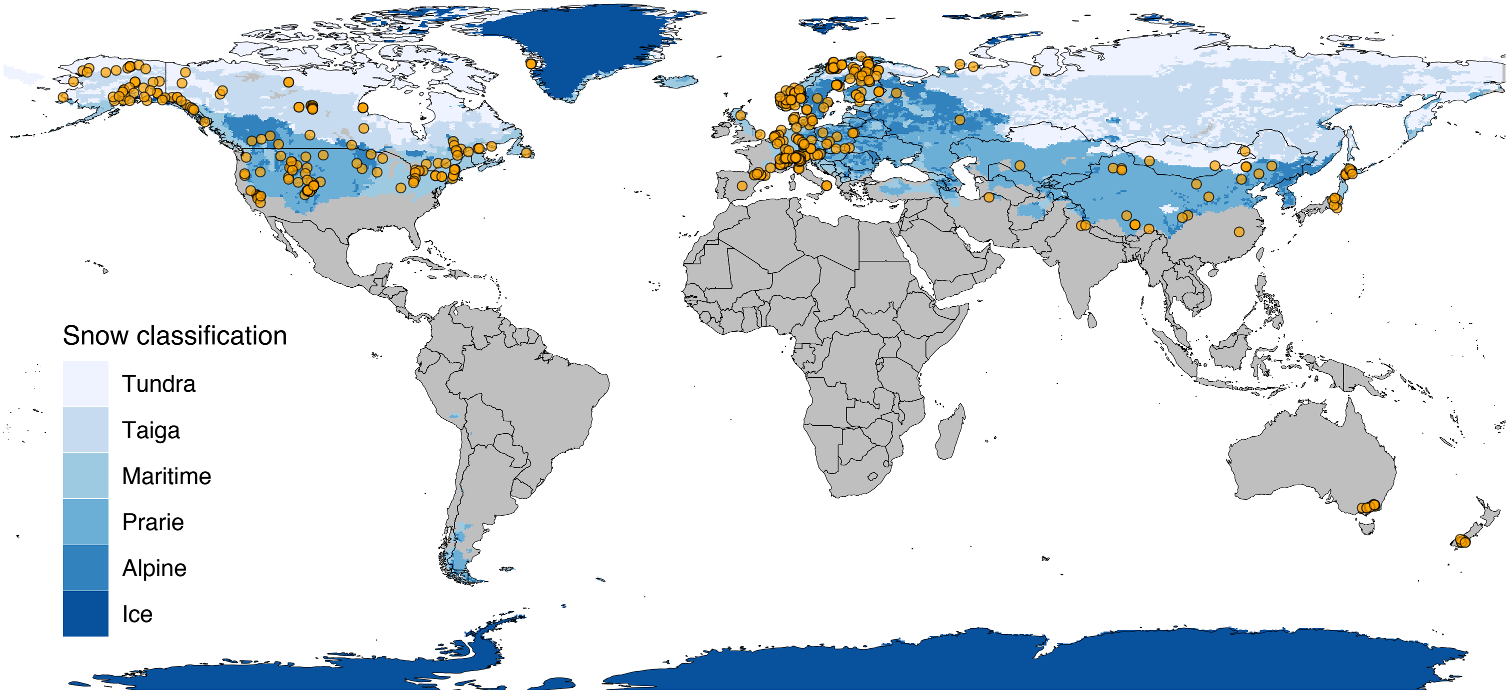
Figure 2. Preferred Reporting Items for Systematic Reviews and Meta-analyses (PRISMA: Moher et al. 2009) flowchart, outlining the process followed to compile the dataset used in the literature review; *n* = number of original research papers (studies).

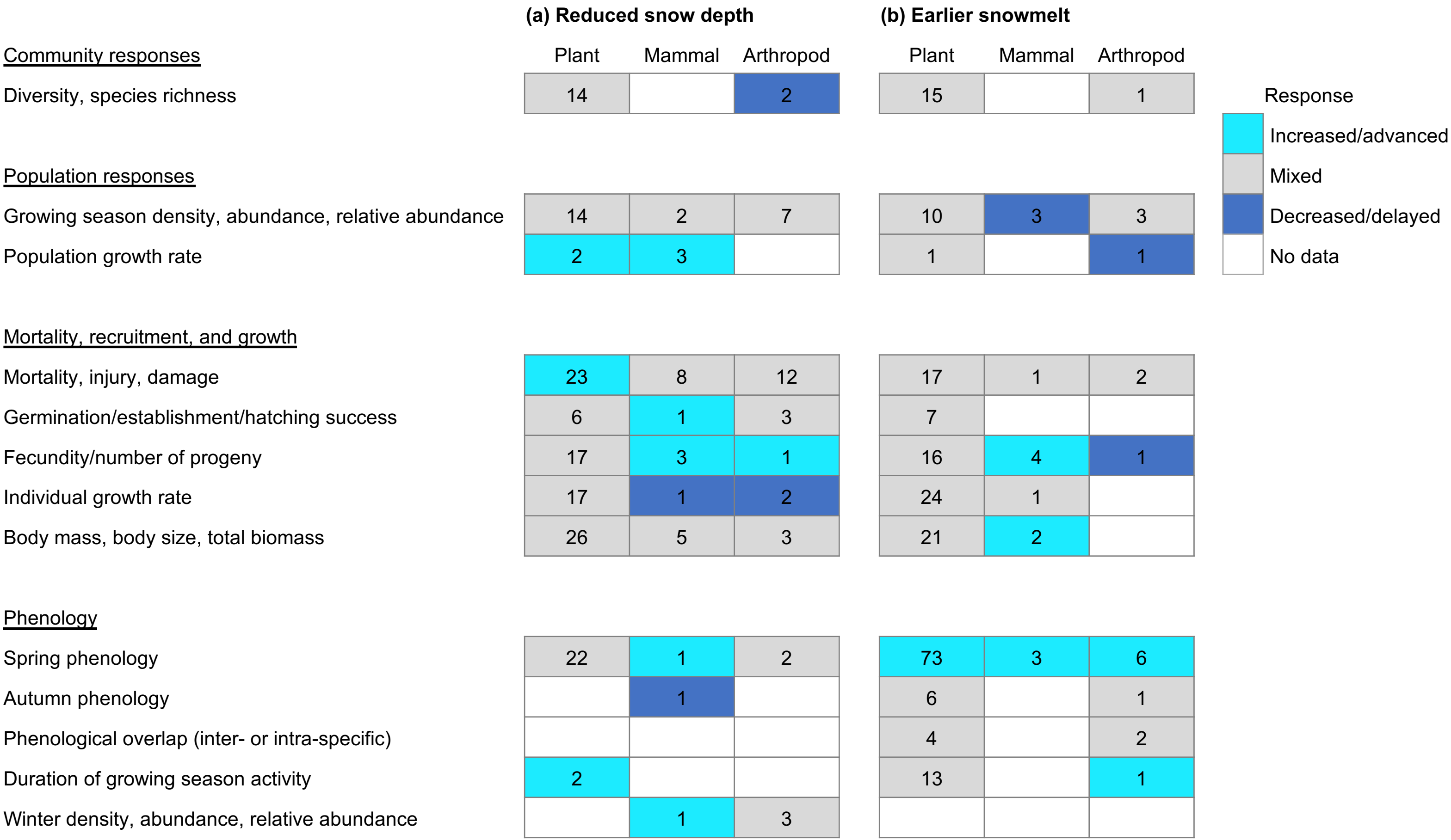
Figure 3. Distribution of study sites in relation to snow type and geography. Colors indicate different snow classifications according to Sturm et al. (1995) and studies included in the review are shown as orange circles. Snow classification data were obtained from the Atlas of the Cryosphere (Maurer 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			