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The subnivium: a deteriorating seasonal refugium

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For many terrestrial organisms in the Northern Hemisphere, winter is a period of resource scarcity and energy deficits, survivable only because a seasonal refugium – the "subnivium" – exists beneath the snow. The warmer and more stable conditions within the subnivium are principally driven by snow duration, density, and depth. In temperate regions, the subnivium is important for the overwintering success of plants and animals, yet winter conditions are changing rapidly worldwide. Throughout the Northern Hemisphere, the impacts of climate change are predicted to be most prominent during the winter months, resulting in a shorter snow season and decreased snow depth. These climatic changes will likely modify the defining qualities of the subnivium, resulting in broad-scale shifts in distributions of species that are dependent on these refugia. Resultant changes to the subnivium, however, will be spatially and temporally variable. We believe that ecologists and managers are overlooking this widespread, crucial, and vulnerable seasonal refugium, which is rapidly deteriorating due to global climate change.

Winter is the season of energy deficits, requiring organisms to either avoid (eg migrate) or confront (eg utilize accumulated somatic stores) an extended period of resource scarcity and extreme environmental conditions. The majority (98%) of the snow-covered area of the globe occurs in the Northern Hemisphere (Figure 1) and its extent is strongly seasonal (Fountain *et al.* 2012), expanding from < 2 million km^2 in August to > 45 million km^2 (30% of Earth's total land surface) in January (Lemke *et al.* 2007). Although the largest, most visible organisms live above the snow, most terrestrial organisms and many ecological processes persist below the snow (Campbell *et al.* 2005). Consequently, the duration and depth of snow cover are critical factors in the overwintering success of many plants and animals (Korslund and Steen 2006).

In a nutshell:

- Beneath the snow there exists an insulated and thermally stable refugium – the subnivium
- Warming winters caused by climate change are reducing the duration, depth, and insulation of snowpack; as a result of altered snow conditions, the subnivium will exhibit increased thermal variability and potentially decreased temperatures
- These changes will have important implications for a diversity of organisms that depend on the subnivium for winter survival
- We predict large-scale distributional shifts of species that are adapted to overwintering in the subnivium because future biophysical changes will exceed their physiological capacity

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■ The anatomy of the "subnivium"

Previous authors have described the "subnivean space" or "subnivean environment" as the interface between the soil and snow (Halfpenny and Ozanne 1989) and the environment under snowpack (Marchand 1996); here, we coin the term "subnivium" to describe the "below snow" seasonal refugium because it provides environmental stability and serves as a habitat to which species can retreat to during changing environmental conditions (Keppel and Wardell-Johnson 2012). The subnivium maintains stable temperatures near freezing because heat released from the soil is trapped by the low thermal conductivity of snow (Figure 2). In addition to hollow spaces beneath logs and other objects that intercept snowfall, a base layer of loose, granular snow exists at the interface between the snowpack and the soil surface. This loose snow is formed by water vapor transport. As heat from the soil slowly migrates upward through the snow layer, it creates a vertical gradient of decreasing temperature (Figure 2). Concurrently, sublimation causes the air within the snowpack to become saturated, and because warmer air holds more water, a gradient of water vapor concentration also forms. As saturated air diffuses upward, it encounters colder temperatures and the water vapor condenses. The result is a continual transport of water molecules upward through the snow, reducing snow crystal size at the base and forming a thermally stable zone of loose, granular snow. This well-insulated and thermally stable environment is reflected by the smaller changes in subnivium temperature relative to changes in air temperature. As snow depth decreases or snow density increases (Figure 2), the insulation provided by the snow is reduced and temperatures in the
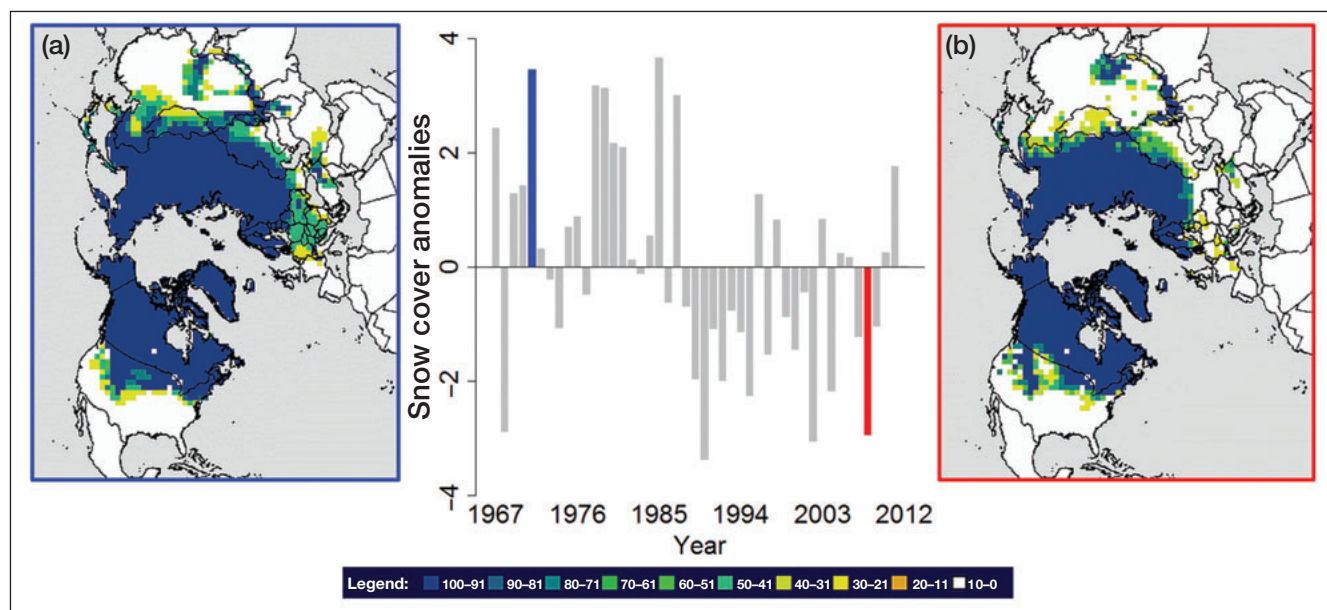
Figure 1. *Northern Hemisphere snow cover extent (SCE) for the month of March between 1966 and 2012. With a long-term average of 40.4 million km², March snow cover anomalies (millions of square kilometers) are becoming increasingly negative and projected to attenuate in the future. The two maps display March SCE (percent of days snow covered) for (a) 1971 and (b) 2008; SCE was about 6 million km² lower in 2008 than in 1971. Data were provided by the Global Snow Laboratory, Rutgers University (accessed 10 Dec 2012).*

subnivium become colder and more variable until they track ambient temperatures.

■ **The subnivium community**

Plant dormancy and metabolic activity

Most herbaceous plants persist through winter by lying dormant as seed or root stock, and by avoiding desiccation and freezing by remaining within the moister and warmer subnivium. Snow removal experiments have shown that snowpack decreases frost penetration into the soil, thereby reducing root damage and plant death during winter (Kreyling *et al.* 2012). Consequently, plant growth in spring is accelerated by a well-structured subnivium, while community composition is strongly affected by the abiotic conditions within the subnivium (Kreyling 2010). The subnivium can also enable plant activity, especially during late winter or early spring (Figure 3a). Elevated carbon dioxide (CO_2) concentrations (in some cases markedly high) and warm temperatures promote photosynthesis and other metabolic activity among the inhabitants of the subnivium (Starr and Oberbauer 2003).

Microbial activity

Long-lasting snow cover insulates surface soils in late winter and can hold soil temperatures above the threshold needed for microbial respiration during some or all of winter (Sullivan *et al.* 2008). Indeed, soil respiration during winter constitutes up to half of the total annual respi-

ration in high-latitude ecosystems (see Larsen *et al.* 2007). Rates of microbial respiration are dependent on snowpack conditions; deeper snow leads to a warmer subnivium, which increases the rate of winter carbon efflux (Monson *et al.* 2005). Microbial activity during winter increases mineralization of organic matter and net mineralization rates are actually at their highest during winter. Microbial activity under a seasonal layer of snow can also play a central role in controlling both surface water and gaseous nitrogen losses (Sullivan *et al.* 2008). Certain types of fungi proliferate in the subnivium, creating extensive mats beneath the snow and even growing vertically into the snow cover. These so-called "snow molds" (Figure 3b) parasitize dormant plants and are important in plant litter decomposition, acquiring nutrients from the organic layer and water and oxygen from the snow (Schmidt *et al.* 2008).

Animal survival

During winter, most invertebrates remain dormant and are either resistant or tolerant to freezing. Freeze-resistant species supercool their bodies and prevent body fluids from freezing by masking or eliminating particles that induce ice formation. Alternatively, freeze-tolerant species survive ice formation by manufacturing proteins that promote extracellular freezing, thereby reducing hazardous intracellular freezing. For both strategies, survival hinges on stable and predictable thermal conditions (Figure 3c). Many invertebrates remain active in the winter (especially those from the Orders Collembola [springtails], Acari [mites and ticks], Coleoptera [beetles],

Araneae [spiders], and Diptera [true flies]); most survive in the subnivium, although a few species will sporadically emerge from the subnivium and be active on the snow surface (Merriam *et al.* 1983; Aitchison 2001). Some invertebrates will forage throughout the winter, feeding on fungal hyphae and spores growing in the subnivium, with their activity increasing from late fall to late winter, as the snowpack develops (Merriam *et al.* 1983).

Most vertebrates inhabiting the subnivium are small (< 250 g), although some larger bodied organisms access the subnivium (Figure 3d) or dens therein (Figure 3e). Insectivorous shrews and herbivorous voles are active in, and some lemmings even reproduce during, the winter months (Duch-esne *et al.* 2011). The conditions of the subnivium, most notably the presence of pockets of green vegetation, drive the abundance and cycling of mammals in some locations (Korslund and Steen 2006). Other species are transient occupants; some gallinaceous birds roost within the subnivium on cold nights, reducing their energetic costs up to threefold, while small-bodied carnivores (particularly *Martes* and *Mustela* spp) use the subnivium both for hunting and resting (Taylor and Buskirk 1994).

Other vertebrates, including omnivorous rodents, hibernate within the stable subnivium, and many amphibians and reptiles exhibit complex physiological responses to facilitate freeze-tolerance (Figure 3f). In below-freezing conditions, these herptiles use nucleators in their blood to initialize formation of extracellular ice (Wolanczyk *et al.* 1990). This ice triggers an increase in circulating glucose, which is taken up by cells to stabilize proteins and prevent freezing damage and osmotic water loss (Storey and Storey 1992). Once sufficient glucose is delivered to the tissues, blood is drained from major organs and the heart ceases to beat (Storey and Storey 1992). Later, as temperatures increase and the animal thaws, circulation is restored and glucose is re-sequestered. These processes are energetically costly; consequently, more variable temperatures can induce increases in metabolic rate (Sinclair *et al.* 2013).

■ Changing winter conditions

The winter climate of the Northern Hemisphere is changing rapidly. From 1906 to 2005, global mean surface temperatures increased by 0.74°C ± 0.18°C, with the majority of increases occurring over inland areas at northern latitudes during winter (December to February) and spring (March to May; Trenberth *et al.* 2007). This warming has led to substantial changes in the extent, duration,
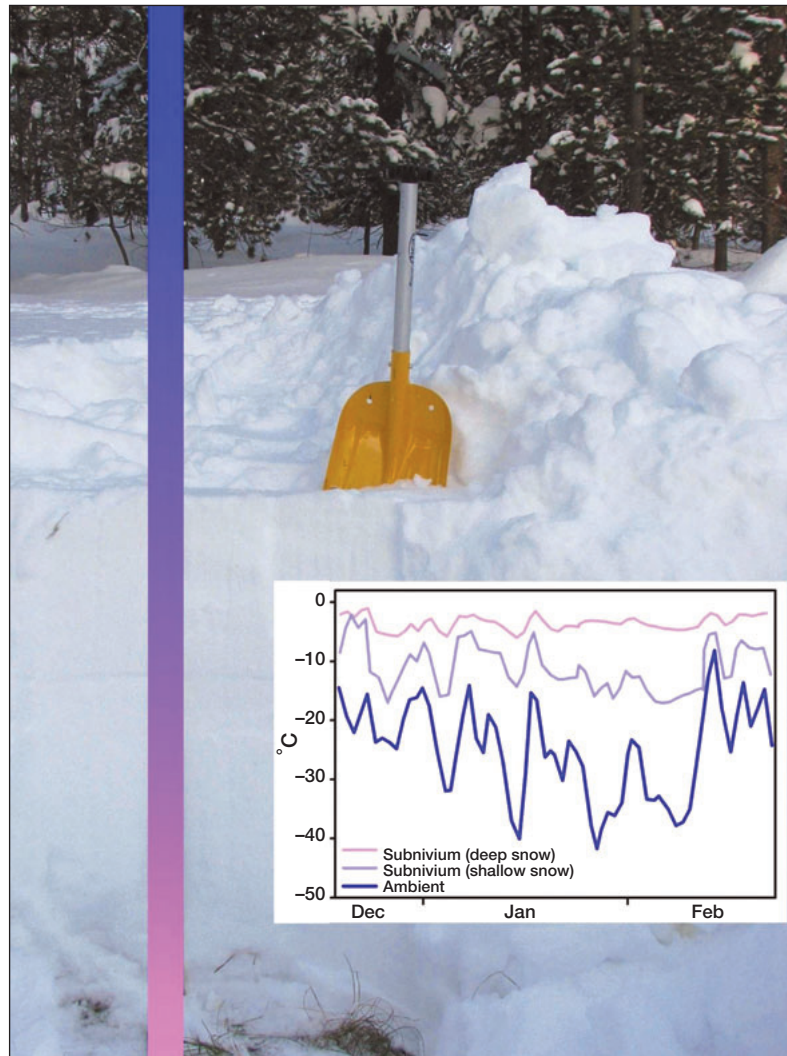

Figure 2. *Minimum daily temperatures beneath deep and shallow snowpack, as compared with ambient temperature, near Bemidji, Minnesota (inset graph). Deep, low-density, undisturbed snow provides an important thermal blanket for the subnivium, increasing temperatures and reducing thermal variability. Graph adapted from Wanek (1974).*

and characteristics of the cryosphere (areas of snow, freshwater and sea ice, glaciers, and frozen ground; Fountain *et al.* 2012). Since the early 1920s, and especially since the late 1970s, the extent of snow cover in the Northern Hemisphere has declined, primarily in spring and summer (Groisman *et al.* 2004). Consequently, the month of maximum snow cover has shifted from February to January and spring melt has advanced by almost two weeks (Dye 2002). Between 1970 and 2010, the rate of decrease in snow cover extent in March and April was 0.8 million km^2 per decade, corresponding to a 7% and 11% decline, respectively (Brown and Robinson 2011). Changing snowfall regimes and reduced ice cover on lakes have increased lake-effect snow in coastal areas (Burnett *et al.* 2003), although these patterns can be influenced by factors such as regional circulation patterns (eg frequency of cold-air outbreaks). For many regions of North America, the duration of the snow season (defined

Figure 3. *Examples of the diversity of subnivium users. (a) Plants like the glacier lily* (Erythronium grandiflorum) *rely on the warm temperatures, high humidity, and elevated CO_2 levels afforded by the subnivium to survive and even grow during winter; (b) microbial activity can be high within the subnivium, where snowmolds (eg* Typhula *sp) can become abundant; (c) many invertebrates, such as the freeze-tolerant woolly bear caterpillar* (Pyrrharctia isabella)*, aestivate within the subnivium; larger-bodied vertebrates like (d) willow ptarmigans* (Lagopus lagopus) *remain active throughout the winter but seek refuge within the subnivium to avoid extreme cold, while (e) other species, such as porcupines* (Erethizon dorsatum)*, seek subnivium dens to reduce thermoregulatory costs; (f) freeze-tolerant herptiles, including wood frogs* (Rana sylvatica)*, are dependent on the subnivium's stable thermal conditions for over-winter survival.*

over much of Canada since 1950 (Brown *et al.* 2007), whereas some countries such as Finland (Hyvärinen 2003) and former republics of the Soviet Union (Ye and Ellison 2003) have experienced increases in maximum snow depth, despite a shorter winter season. Although snowpack depth may increase in some locations, the proportion of precipitation falling as rain instead of snow will likely increase, leading to denser and less insulating snow cover. Because temperatures stabilize beneath deep snow, reduced and late accumulating or denser snow cover will create a colder and more variable subnivium. Winter field experiments have demonstrated that reduced snowpack can lead to lower soil temperatures, advanced snowmelt, and a greater number of frost days (Wipf *et al.* 2009). Indeed, winter air temperatures have progressively increased in the Upper Midwest of the US, but winter soil temperatures have decreased (Isard *et al.* 2007), likely because of reduced snowpack thicknesses and persistence of snow cover (Brown and DeGaetano 2011). However, attenuating ambient temperatures may offset the reduction in thermal insulation from snowpack loss, with depth of soil freezing exhibiting little or no change (Campbell *et al.* 2010).

Recently, Sinha and Cherkauer (2010) constructed a macroscale land-surface model and simulated cold-season variables, including soil frost, and found that within 100 years, the number of regional freeze–thaw cycles at the soil level will likely increase. Similarly, Mellander *et al.* (2007) predicted that soil freeze–thaw events in Sweden will increase by > 30% within this century. Despite these forecasts, many questions remain as to which suite of biophysical characteristics are most important for the maintenance of the subnivium and how they will be altered as a consequence of climate-change-induced warming. For much of the Northern Hemisphere, winter warming will likely reduce snowpack, increase snow density, and shorten the duration of snow cover and, consequently, cause important changes to the subnivium. Ultimately, despite warming ambient winter air temperatures, the subnivium will gradually change to a colder and more thermally variable environment (Figure 4).

as the period where snow is more likely than rain) has decreased by > 1.5 months (Lorenz *et al.* 2009), with the largest reduction in snow cover occurring during the March–April period (Lemke *et al.* 2007). In northern Europe, warming winters are predicted to result in 40–80% fewer days of snow cover by the end of this century (Jylha *et al.* 2008).

Widespread changes in snow depth have already been documented for many regions. Snow depth has declined

Geographic variation in climate change

Climate change is a geographically heterogeneous and dynamic process; as a result, future changes to the subnivium will be region-specific. In southern Canada and western Russia, the fraction of total annual precipitation that falls as snow is declining (Groisman *et al.* 2004), but in other regions north of 55°N (eg Alaska, Finland) there has been little change in the fraction of precipitation that is snow (Trenberth *et al.* 2007). Snow cover dynamics in mountain regions are often characterized by large regional and altitudinal variations (Räisänen 2007), and although regional models predict that snow-season length and snow depth are very likely to decrease across most of North America, the northernmost part of Canada is expected to experience increases in maximum snow depth (Christensen *et al.* 2007). Models generally agree that the winter climate of the Northern Hemisphere will change considerably.

At a local scale, variations in land cover will ameliorate or exacerbate changes in the subnivium. Differences in vegetation cover profoundly influence thermal regimes and snow characteristics. For example, Suggitt *et al.* (2011) found that winter ground-level minimum temperatures in heathland and grassland were 4–6°C cooler than in woodlands. Thus, wooded habitats appear to moderate ground-level temperature variability relative to unforested lands. Notably, this microclimatic variation exceeds estimates of warming under any of the Intergovernmental Panel on Climate Change greenhouse-gas emissions scenarios. Forest cover can also alter both snow accumulation and snowmelt processes, mostly by intercepting snowfall and modifying the surface micrometeorology (Musselman *et al.* 2008; Andreadis *et al.* 2009). Despite evidence of geographic and land-cover effects on snow depth and microclimates, most attempts to understand the regional effects of climate change on biological communities have not incorporated regional replication, microclimatic effects, or the synergistic influences of land cover.

Ecological consequences of climate change on subnivium species

Colder and more variable temperatures within the subnivium will have major impacts on biotic communities that have evolved under mild and stable conditions. Colder temperatures and more freeze–thaw cycles can cause ice damage in above- and belowground plant tissue, increasing plant mortality, delaying flowering, and reducing plant biomass (Foresman *et al.* 1976); this is also the
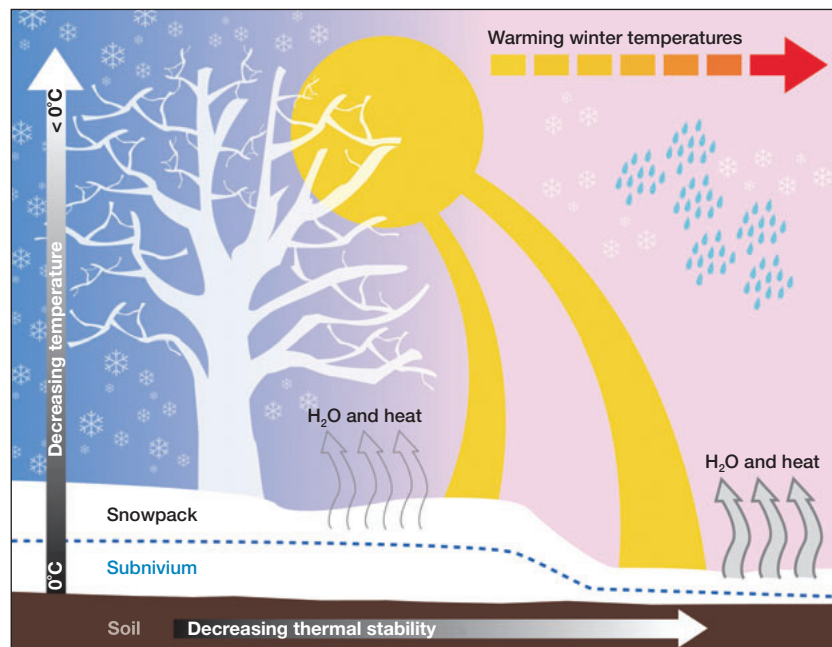

Figure 4. Conceptual diagram depicting the mechanistic pathways leading to the development and maintenance of the subnivium and possible changes to abiotic conditions within this seasonal refugium as a result of warming winters due to climate change.

case for cold-tolerant coniferous trees (Sutinen *et al.* 1999). The impacts of a changing subnivium will not be limited to sessile organisms. For example, Neumann and Merriam (1972) calculated that a decrease of 3°C in the subnivium would raise the metabolic demand of the northern short-tailed shrew (*Blarina brevicauda*) by ~25 calories hr^{-1}, making the subnivium a potentially energetically prohibitive environment for this species. Through experimental manipulation, Korslund and Steen (2006) found that tundra vole (*Microtus oeconomus*) survival was directly linked to subnivium quality; Kausrud *et al.* (2008) demonstrated that altered conditions in the subnivium as a result of changing regional weather drove the population cycling of alpine rodents in Fennoscandia.

Because the overwintering strategies of invertebrates vary widely in terms of their biochemistry and physiology (Bale and Hayward 2010), it is difficult to predict how each species will respond. Reduced snow cover will clearly be detrimental to some species (Bale and Hayward 2010). On the other hand, colder subnivium temperatures can reduce metabolic activity for some overwintering invertebrates, reducing consumption of stored energy and leading to improved body condition (Marshall and Sinclair 2012). Nevertheless, worsening conditions in the subnivium have the potential to greatly alter community composition, given that they will be deleterious to some species and beneficial to others.

Freeze-tolerant herptiles are one of the groups most likely to be sensitive to a deteriorating subnivium. Below −8°C, uncontrolled ice formation within tissues will cause cellular dehydration, damage, and necrosis, which can lead to death while the animal is frozen (Storey and

Storey 1992). In addition, more variable temperatures will likely cause more frequent freeze–thaw cycles, each of which incurs a large energetic cost for the animals. Because the presence of food particles in the gut may prompt uncontrolled ice nucleation (Storey and Storey 1992), herptiles cannot eat to replenish energy lost during freeze–thaw cycles. Thus, reduced energy stores can lead to mortality as a result of excessive internal ice formation while the animal is frozen (due to the lack of glucose, which acts as a cryoprotectant; Jenkins and Swanson 2005), or while the animal is thawed because glucose stores necessary for metabolic functioning are depleted (Sinclair *et al.* 2013). Reduced glucose stores may also negatively affect reproductive output, especially since breeding generally commences immediately after overwintering, while animals are still fasting (Sinclair *et al.* 2013).

Amphibians can tolerate only a very narrow range of temperatures and have limited dispersal abilities, making them particularly vulnerable to climate change (Lawler *et al.* 2010). Survival of juvenile amphibians can be the most important driver of population dynamics and exposure to cold temperatures during the winter months is an important cause of juvenile mortality (Berven 1990); projected changes in snow cover could therefore affect the viability of herptiles throughout their ranges. Thus, altered winter conditions across much of the Northern Hemisphere will likely reduce the extent of important seasonal refugia and create harsher conditions for organisms that depend on the subnivium for overwintering.

■ Future research

Next-generation warming experiments

Experimentation will play a critical role in identifying the ecological impacts and biological mechanisms linked to climate change. Because many physiological responses of plants and animals are limited by temperature, laboratory and greenhouse experiments have been used to simulate future climate conditions. Experimental designs that aim to facilitate the understanding of climate-change impacts are abundant and range from traditional greenhouses to field-based, open-top chambers that let in ambient light and rainfall.

Most of these experiments have focused on measuring plant productivity and biomass, and have been limited in their ability to manage the complexity of multiple species, changing biophysical conditions, and seasonal variability. "Next-generation warming experiments" are becoming increasingly common and are a major focus of simulating climate-change impacts in natural systems. For example, the EVENT experiments are large-scale field experiments designed to test the effects of extreme weather and plant diversity on the performance of individual plant species in experimental communities (Jentsch *et al.* 2007). EVENT manipulations simulate recurrent 100-year extreme events (eg drought, heavy rain, freeze–thaw cycles) by means of rain-out shelters, portable irrigation systems, and buried heating wires. Increasingly common Free Air Carbon dioxide Enrichment (FACE) experiments use massive diffusers to elevate CO_2 concentrations across large areas. Likewise, the Spruce and Peatland Responses Under Climatic and Environmental Change (SPRUCE) experiment focuses on the effects of increased temperature and elevated atmospheric CO_2 concentrations on northern peatland ecosystems. This large-scale experiment evaluates the response of existing biological communities to a range of warming levels via large, modified open-top chambers. Winter experimental studies are far less common, however, and most are conducted on permafrost systems at extreme latitudes (Hannah 2011).

Ecological niche modeling

Mechanistic niche modeling is an important tool for predicting the potential responses of species to future climate change. Traditionally, mechanistic models define an organism's ecological niche as a set of behavioral, morphological, and physiological traits (Kearney and Porter 2009). Modeling the biophysical niche of an organism requires detailed knowledge of its thermoregulatory characteristics and morphological properties, and how both interact with local environmental variables, such as air temperature and solar radiation. By relying on heat and mass transfer equations to develop landscape maps of energetic costs, mechanistic models have been used to simulate the thermoregulatory and distributional effects of heat stress on amphibians and reptiles in lower latitudes but have not been well-integrated into winter ecology studies. Mechanistic niche models offer a particularly useful method for mapping suitable conditions for obligate species within the subnivium (Kearney and Porter 2009).

A united framework

Next-generation experiments and mechanistic niche modeling have greatly advanced our understanding of climate change and its implications for ecological systems. However, these approaches have largely operated independently. Climate-change research would greatly benefit from a unified analytical approach. For example, field experimentation directed at quantifying biophysical properties of the subnivium and at simulating future thermal and precipitation patterns through the use of next-generation technologies could be applied to identify the biophysical drivers of the subnivium. Resultant data could also be used to power species-specific bioclimatic niche models to predict how future subnivium conditions will impact the distribution and abundance of species dependent on the subnivium for overwinter survival. In this way, empirical data from emerging field experiments

could be combined with large-scale metrics of plant and animal survival along existing geographical gradients to predict the future distribution of suitable conditions for subnivium-dependent species.

■ Management implications

The subnivium provides a stable and predictable seasonal habitat for a diversity of overwintering organisms and a variety of ecological processes. Because of macroscale changes in winter conditions as a result of climate change, the subnivium is likely to deteriorate in both extent and quality. These effects will be especially severe along the trailing edge of the cryosphere (that is, in regions that experience considerable but seasonal snow cover). For species whose distributions coincide with these regions, reductions in snow depth and duration may cause a complete loss of their overwintering refugium. Changes to the subnivium will affect species differently but will be particularly detrimental to those species that cannot adapt to the loss of the subnivium or that are unable to track the subnivium's retreating boundary.

Although the winter landscape is often not a primary consideration when setting conservation or management priorities, we believe that changes to or loss of the subnivium represent a major and expanding type of habitat loss and degradation that has previously been largely overlooked. Environmental managers should begin to include the subnivium in their management plans. This will require a conceptual realignment of the spatial and temporal scale of management that recognizes winter as an important biological period in need of protection and monitoring. Rather than regarding the winter landscape as a homogeneous blanket of snow, ecologists and managers should visualize it as a mosaic of micro-refugia for a range of organisms, varying in quality across habitats, aspect, topology, and time. Introducing management actions aimed at mitigating the impacts of global climate change on the subnivium will be difficult to do locally. However, land managers can address site-specific threats (eg recreational snowmobiling or skiing) that compact snow and contribute to the destruction of the subnivium (Wanek 1974). Managers can also promote conditions that enhance the quality and persistence of the subnivium; for example, increasing forest cover moderates ground temperatures (Suggitt *et al.* 2011) and prolongs snow cover (Musselman *et al.* 2008). Consequently, many of the techniques used by managers in the past (eg habitat manipulation) can also be applied to the protection of the subnivium.

■ Acknowledgements

■ References

Aitchison CW. 2001. The effect of snow cover on small animals. In: Jones HG, Pomeroy JW, Walker DA, and Hoham RW (Eds). Snow ecology: an interdisciplinary examination of snow covered ecosystems. Cambridge, UK: Cambridge University Press.

Andreadis KM, Storck P, and Lettenmaier DP. 2009. Modeling snow accumulation and ablation processes in forested environments. *Water Resour Res* **45**: e1–e13.

Bale JS and Hayward SAL. 2010. Insect overwintering in a changing climate. *J Exp Biol* **213**: 980–94.

Berven KA 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* **71**: 1599–1608.

Brown PJ and DeGaetano AT. 2011. A paradox of cooling winter soil surface temperatures in a warming northeastern United States. *Agr Forest Meteorol* **151**: 947–56.

Brown RD and Robinson DA. 2011. Northern Hemisphere spring snow cover variability and change over 1922–2010 including an assessment of uncertainty. *Cryosphere* **5**: 219–29.

Brown R, Derksen C, and Wang L. 2007. Assessment of spring snow cover duration variability over northern Canada from satellite datasets. *Remote Sens Environ* **111**: 367–81.

Burnett AW, Kirby ME, Mullins HT, and Patterson WP. 2003. Increasing Great Lake-effect snowfall during the twentieth century: a regional response to global warming? *J Climate* **16**: 3535–42.

Campbell JL, Ollinger SV, Flerchinger GN, *et al.* 2010. Past and projected future changes in snowpack and soil frost at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Hydrol Process* **24**: 2465–80.

Campbell JL, Mitchell MJ, Groffman PM, *et al.* 2005. Winter in northeastern North America: a critical period for ecological processes. *Front Ecol Environ* **3**: 314–22.

Christensen JH, Hewitson B, Busuioc A, *et al.* 2007. Regional climate projections. In: Solomon S, Qin D, Manning M, *et al.* (Eds). Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK, and New York, NY: Cambridge University Press.

Duchesne D, Gauthier G, and Berteaux D. 2011. Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia* **167**: 967–80.

Dye DG. 2002. Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000. *Hydrol Process* **16**: 3065–77.

Foresman CL, Ryerson DK, Walejko RN, *et al.* 1976. Effect of snowmobile traffic on bluegrass (*Poa pratensis*). *J Environ Qual* **5**: 129–31.

Fountain AG, Campbell JL, Schuur EAG, *et al.* 2012. The disappearing cryosphere: impacts and ecosystem responses to rapid cryosphere loss. *BioScience* **62**: 405–15.

Groisman PY, Knight RW, Karl TR, *et al.* 2004. Contemporary changes of the hydrological cycle over the contiguous United States: trends derived from in situ observations. *J Hydrometeorol* **5**: 64–85.

Halfpenny JC and Ozanne RD. 1989. Winter: an ecological handbook. Boulder, CO: Johnson Books.

Hannah LJ. 2011. Climate change biology. Burlington, MA: Academic Press.

Hyvärinen V. 2003. Trends and characteristics of hydrological time series in Finland. *Nord Hydrol* **34**: 71–90.

Isard SA, Schaetzl RJ, and Andresen JA. 2007. Soils cool as climate warms in the Great Lakes region: 1951–2000. *Ann Assoc Am Geogr* **97**: 467–76.

Jenkins JL and Swanson DL. 2005. Liver glycogen, glucose mobi-

lization and freezing survival in chorus frogs, *Pseudacris triseriata*. *J Therm Biol* **30**: 485–94.

Jentsch A, Kreyling J, and Beierkuhnlein C. 2007. A new generation of climate-change experiments: events, not trends. *Front Ecol Environ* **5**: 365–74.

Jylha K, Fronzek S, Tuomenvirta H, *et al.* 2008. Changes in frost, snow and Baltic Sea ice by the end of the twenty-first century based on climate model projections for Europe. *Climatic Change* **86**: 441–62.

Kausrud KL, Mysterud A, Steen H, *et al.* 2008. Linking climate change to lemming cycles. *Nature* **456**: 93–98.

Kearney M and Porter W. 2009. Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecol Lett* **12**: 334–50.

Keppel G and Wardell-Johnson GW. 2012. Refugia: keys to climate change management. *Glob Change Biol* **18**: 2389–91.

Korslund L and Steen H. 2006. Small rodent winter survival: snow conditions limit access to food resources. *J Anim Ecol* **75**: 156–66.

Kreyling J. 2010. Winter climate change: a critical factor for temperate vegetation performance. *Ecology* **91**: 1939–48.

Kreyling J, Haei M, and Laudon J. 2012. Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. *Oecologia* **168**: 577–87.

Larsen KS, Grogan P, Jonasson S, and Michelsen A. 2007. Respiration and microbial dynamics in two subarctic ecosystems during winter and spring thaw: effects of increased snow depth. *Arct Antarct Alp Res* **39**: 268–76.

Lawler JJ, Shafer SL, and Blaustein AR. 2010. Projected climate impacts for the amphibians of the Western Hemisphere. *Conserv Biol* **24**: 38–50.

Lemke P, Ren J, Alley RB, *et al.* 2007. Observations: changes in snow, ice and frozen ground. In: Solomon S, Qin D, Manning M, *et al.* (Eds). Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK, and New York, NY: Cambridge University Press.

Lorenz DJ, Vavrus SJ, Vimont DJ, *et al.* 2009. Wisconsin's changing climate: temperature. In: Pryor SC (Ed). Understanding climate change: climate variability, predictability, and change in the midwestern United States. Bloomington, IN: Indiana University Press.

Marchand PJ. 1996. Life in the cold: an introduction to winter ecology, 3rd edn. Hanover, NH: University Press of New England.

Marshall KE and Sinclair BJ. 2012. Threshold temperatures mediate the impact of reduced snow cover on overwintering freeze-tolerant caterpillars. *Naturewissenschaften* **99**: 33–41.

Mellander PE, Lofvenius MO, and Laudon H. 2007. Climate change impact on snow and soil temperature in boreal Scots pine stands. *Climatic Change* **85**: 179–93.

Merriam G, Wegner J, and Caldwell D. 1983. Invertebrate activity under snow in deciduous woods. *Holarctic Ecol* **6**: 89–94.

Monson RK, Lipson DL, Burns SP, *et al.* 2005. Winter forest soil respiration controlled by climate and microbial community composition. *Nature* **439**: 711–14.

Musselman KN, Molotch NP, and Brooks PD. 2008. Effects of veg-

etation on snow accumulation and ablation in mid-latitude sub-alpine forest. *Hydrol Process* **22**: 2767–76.

Neumann PW and Merriam HG. 1972. Ecological effects of snowmobiles. *Can Field Nat* **86**: 207–12.

Räisänen J. 2007. Warmer climate: less or more snow? *Clim Dynam* **30**: 307–19.

Schmidt SK, Wilson KL, Meyer AF, *et al.* 2008. Phylogeny and ecophysiology of opportunistic "snow molds" from a subalpine forest ecosystem. *Microb Ecol* **56**: 681–87.

Sinclair BJ, Stinziano JR, Williams CM, *et al.* 2013. Real-time measurement of metabolic rate during freezing and thawing of the wood frog, *Rana sylvatica*: implications for overwinter energy use. *J Exp Biol* **216**: 292–302.

Sinha T and Cherkauer KA. 2010. Impacts of future climate change on soil frost in the midwestern United States. *J Geophys Res* **115**: e1–e16.

Starr G and Oberbauer SF. 2003. Photosynthesis of Arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology* **84**: 1415–20.

Storey KB and Storey JM. 1992. Natural freeze tolerance in ectothermic vertebrates. *Annu Rev Physiol* **54**: 619–37.

Suggitt AJ, Gillingham PK, Hill JK, *et al.* 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* **120**: 1–8.

Sullivan PF, Welker JM, Arens SJT, and Sveinbjörnsson B. 2008. Continuous estimates of CO_2 efflux from arctic and boreal soils during the snow-covered season in Alaska. *J Geophys Res* **113**: e1–e11.

Sutinen ML, Holappa T, Ritari A, and Kujalal K. 1999. Seasonal changes in soil temperature and snow-cover under different simulated winter conditions: comparison with frost hardiness of Scots pine (*Pinus sylvestris*) roots. *Chemosphere: Global Science Change* **1**: 485–92.

Taylor SL and Buskirk SW. 1994. Forest microenvironments and resting energetics of the American marten *Martes americana*. *Ecography* **17**: 249–56.

Trenberth KE, Jones PD, Ambenje P, *et al.* 2007. Observations: surface and atmospheric climate change. In: Solomon S, Qin D, Manning M, *et al.* (Eds). Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK, and New York, NY: Cambridge University Press.

Wanek WJ. 1974. The ecological impact of snowmobiling in northern Minnesota. Proceedings of the Snowmobile and Off the Road Vehicle Research Symposium. East Lansing, MI: Michigan State University.

Wipf S, Stoeckli V, and Bebi P. 2009. Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change* **94**: 105–21.

Wolanczyk JP, Storey KB, and Baust JG. 1990. Ice nucleating activity in the blood of the freeze-tolerant frog, *Rana sylvatica*. *Cryobiology* **27**: 328–35.

Ye HC and Ellison M. 2003. Changes in transitional snowfall season length in northern Eurasia. *Geophys Res Lett* **30**: 1252, doi:10.1029/2003GL016873