The Ecological Importance of Winter in Temperate, Boreal, and Arctic Ecosystems in Times of Climate Change

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Contents

Abstract Climate warming is strongest in winter and in northern ecosystems. Ecological and biogeochemical impacts, however, depend mainly on soil temperatures. Climate warming can contrastingly affect winter soil conditions across northern biomes due to the crucial importance of snow cover: Increasing winter precipitation results in soil warming in the arctic, while midwinter snowmelt events can induce more severe soil frost in arctic and boreal ecosystems. Cold-temperate ecosystems are projected to experience increased soil frost due to strongly reduced snow cover no longer insulating the soil against still cold air temperatures. In cool-temperate ecosystems, warming eventually causes the complete loss of soil frost. Both pathways, soil warming and soil cooling, have important implications for ecology and biosphere-atmosphere feedbacks: In arctic and boreal ecosystems,

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increased decomposition and mineralization allow for enhanced primary production, but midwinter melting followed by frost and/or rain-on-snow events might counteract this trend. More variable surface temperatures can damage primary production, and colder soil temperatures, due to reduced snow cover, can significantly decrease decomposition in cold-temperate ecosystems. For cool-temperate ecosystems, wetter winters could result in nutrient leaching, and altered dormancy patterns could cause increased frost damage despite air warming. In summary, winter processes are clearly relevant for the biosphere-atmosphere feedback, and even the sign of this feedback, i.e., ecosystems acting as carbon sink or as carbon source, depends on winter processes in temperate, boreal, and arctic ecosystems. This review concludes that current knowledge is not sufficient to quantify this feedback with satisfactory certainty. Important processes and the key uncertainties are identified, e.g., synchronicity in above- versus belowground growing season; temporal hierarchies in ecological processes such as the role of root damage and root activity for decomposition of soil organic matter ("priming"); or shifts in plant species composition due to winter climate change determining primary production as well as litter quantity and decomposability. Evidently, sound projections of future ecosystem functioning and biotic feedbacks to climate change require a comprehensive understanding of winter ecological processes, which have so far too often been neglected.

1 Winter Climate Change

1.1 Air Temperature

Climate records and climate models consistently project polar amplification in air temperature warming of the Northern Hemisphere, implying increased rates of warming from tropical to polar regions (Stocker 2014). Furthermore, warming in winter is expected to exceed warming in all other seasons (Stocker 2014). Winter warming will exceed annual warming for arctic (app. 4.4 and 3.4 K, respectively), boreal (app. 3.8 and 3.0 K, respectively), and temperate (app. 2.7 and 2.6 K, respectively) ecosystems until 2100 according to 42 CMIP5 global models for the RCP4.5 scenarios (Stocker 2014). However, occasional cold winter extremes will continue to occur despite this general warming trend (Pachauri and Mayer 2015). For Europe, such events might even increase in frequency as future warming of the Polar Ocean might increase advection of polar air masses, causing cold extremes over Europe (Petoukhov and Semenov 2010; Yang and Christensen 2012).

1.2 Precipitation

Winter precipitation is generally expected to increase, again, with largest increases toward the poles (Stocker 2014). For Northern Asia, for instance, this increase is projected to be more than 50%, whereas summer precipitation is projected to hardly change (Stocker 2014).

Ecologically more important than a general increase in precipitation amount, however, are shifts in the form of precipitation. Snowfall is declining at the geographical margins of seasonal snowfall occurrence but increasing toward regions with colder winters in North America (Kunkel et al. 2009). Likewise, snowfall in Canada is increasing toward the North and decreasing toward the South of the country (Mekis and Vincent 2011). Similar patterns are reported for Europe and Japan (Scherrer and Appenzeller 2006; Takeuchi et al. 2008). Taken together, winters in temperate regions are expected to become wetter, while winters in boreal and arctic regions are expected to become snowier.

1.3 Snow

More than half (55%) of the land area of the Northern Hemisphere is influenced by seasonal snow cover (Zhang et al. 2003). Snow cover, however, is declining by 5.3 days per decade since winter 1972–1973 (Choi et al. 2010). Largest decreases occur in regions with winter mean air temperatures in the range of −5 to +5°C around the mid-latitudinal coastal margins of the continents (Brown and Mote 2009). Snow cover will continue to further shrink by 7% for RCP2.6 and by 25% in RCP8.5 by the end of the twenty-first century for the multi-model average, with strongest changes in advancing spring snowmelt (Brown and Mote 2009; Brutel-Vuilmet et al. 2013).

Snow depth and the snow water equivalent, however, are more sensitive to snowfall amount than snow cover (Brown and Mote 2009). For Eurasia, for instance, winter snow accumulation is currently increasing, but snowmelt is occurring earlier and quicker (Bulygina et al. 2010). With regard to maximum snow depth, model projections are mixed and come with little confidence (Stocker 2014). According to available models, snow depth will increase or only marginally decrease in the coldest regions, while annual maximum snow depth will decrease strongly closer to the southern limit of the (formerly) seasonally snow-covered area (Brutel-Vuilmet et al. 2013; Demaria et al. 2016; Estilow et al. 2015; Raisanen 2008).

1.4 Soil Temperature

Many relevant ecological processes are driven by winter soil temperatures, e.g., biogeochemistry or overwintering of organisms (Kreyling 2010). Despite this high ecological importance, soil temperatures are not even considered in the reports of the Intergovernmental Panel on Climate Change (IPCC) apart from the projected degradation of permafrost (Stocker 2014). Soil temperature shifts with climate change are complex, because soil temperature depends in nontrivial ways both on air temperature and precipitation changes as soils are protected from air frost events if the insulating snow cover is sufficiently deep and continuous (Groffman et al. 2001; Sturm et al. 1997). This insulating power of snow is well known and can prevent soils from freezing temperatures even considering winter conditions in boreal regions (Isard and Schaetzl 1998). Already 30–40 cm of powder snow can effectively decouple air and soil temperature (Sturm et al. 1997). However, the insulating power of snow cover changes with the degradation of the snow. Compaction, for instance, can completely remove its insulation power, and soils under ski pistes are consequently much colder than outside the prepared areas (Rixen et al. 2004; Steinbauer et al. 2017).

Decreased insulation by snow cover could expose soils to cold air temperatures either overnight or during cold snaps, resulting in the apparent paradox of "colder soils in a warmer world" (Groffman et al. 2001). In light of the ongoing and projected changes in air temperature and snow cover/depth outlined above, this phenomenon is to be expected for regions where air temperatures continue to drop below zero degrees centigrade and snow cover is missing, i.e., focus on the temperate regions formerly experiencing continuous snow cover but now falling out of the seasonally snow-covered area (from here on referred to as cold-temperate). Here, e.g., in Southern Canada, the Northeast United States, or southern Scandinavia and northeastern Central Europe, soil minimum temperatures may actually become colder, and frequency of freeze-thaw cycles is increasing with climate change (Brown and DeGaetano 2011; Campbell et al. 2010; Henry 2008). Further south (from here on referred to as cool-temperate), e.g., across large parts of Central Europe, the increase in air temperature makes more than up for the decreasing snow cover, and soil minimum temperatures are rising even stronger than mean air temperatures, while soil freeze-thaw cycles are becoming less frequent (Kreyling and Henry 2011).

Boreal and arctic regions might experience soil warming due to the insulating effect of increased snow cover (Iijima et al. 2010). Here, however, temporal variability of winter weather may become ecologically important if widespread snowmelt events during winter increase in frequency, e.g., due to more frequent occurrence of warm air masses over some Arctic regions in winter (Visbeck et al. 2001).

Another ecologically relevant scenario of winter precipitation change are increases in the frequency of rain-on-snow events, which can cause the formation of massive and gas-impermeable ice covers (Bieniek et al. 2018) and reduce the insulation capacity of the snow cover (Martz et al. 2016).

2 Ecosystem Responses to Winter Climate Change

Winter processes can have substantial ecological effects on seasonally snow-covered ecosystems, as originally demonstrated for the Arctic (Clein and Schimel 1995). We have shown that winter climate can have stronger effects on dissolved and gaseous carbon (C) emissions of a wet boreal forest than summer climate (Haei et al. 2013). Likewise, temperate ecosystems are strongly shaped by seasonal cycles, with the winter season being a major ecological filter and driver (Campbell et al. 2005; Kreyling 2010). Snow provides a relatively mild subnivean microclimate for plants, animals, and soil beneath (Kausrud et al. 2008; Pauli et al. 2013). Changes in snow cover, consequently, affect ecological processes. In particular, soil freezing in response to decreased snow cover has been identified as crucial parameter which can disrupt soil microbial activity (Bolter et al. 2005; Yanai et al. 2004), damage plant roots (Tierney et al. 2001; Weih and Karlsson 2002), and lead to increased soil nitrogen (N) leaching (Joseph and Henry 2009), increased soil trace gas losses (Matzner and Borken 2008), decreased plant productivity (Schuerings et al. 2014), and plant mortality (Schaberg et al. 2008; Buma et al. 2017). Freezing can also affect soil physical processes directly by breaking up soil aggregates (Oztas and Fayetorbay 2003) and by reducing soil water infiltration (Iwata et al. 2010).

Despite the fact that studies focusing on winter ecology report its high relevance, comparably few ecological studies on the effects of climate change consider winter at all (Fig. 1). More than two thirds of studies on ecological responses to climate change in arctic ecosystems, where the importance of winter is hardly arguable, ignore winter effects, and this share further increases for boreal and temperate ecosystems (Fig. 1). This pattern appeared to change in 2010, when a strong increase in climate impact studies in temperate and arctic ecosystems took winter into account (Fig. 2). However, this increase did not sustain and the number of studies considering winter rather stagnated, in particular compared to the overall number of scientific papers on climate change effects in these biomes (inserted panel in Fig. 2). The following review of ecological responses to winter climate change is therefore fragmentary. Primary production has been studied in some detail, but these studies rather demonstrate high complexity in the relevant processes than a coherent trend (Sect. 2.1). There is also quite some knowledge available on soil biotic activity,

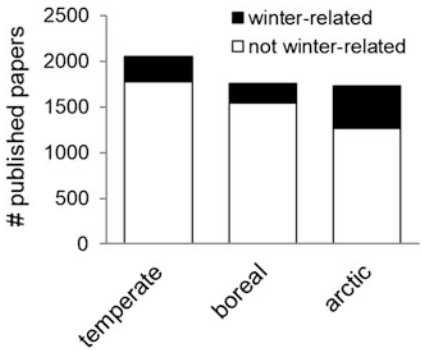

Fig. 1 Published research on biogeochemical and ecological impacts of climate change separated by papers dealing with effects of winter climate change (search string in ISI Web of Science: =((winter or frost or snow or freez∗) and ("climate change" or "climatic change" or "global warming" or "climate warming") and (biogeochemi∗ or "primary product∗" or "biomass" or "decomposition" or "mineralization") and (boreal or arctic or temperate)); articles only) versus climate change in other seasons (search string in ISI Web of Science identical to the one above but without "(winter or frost or snow or freez∗) and")

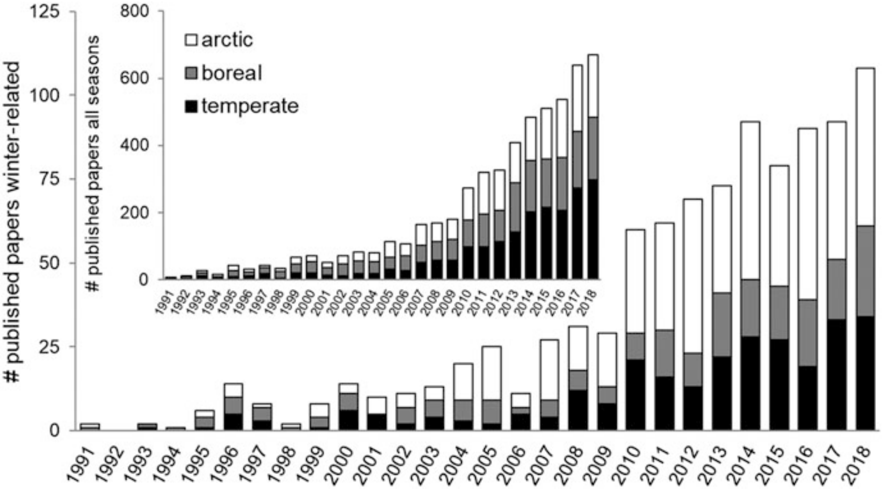

Fig. 2 Temporal development of published research on biogeochemical and ecological impacts of climate change separated by papers dealing with effects of winter climate change (main graph) versus climate change effects in all seasons (inlay). Search strings in ISI Web of Science identical to Fig. 1

decomposition, and mineralization in response to the expected changes in winter climate (Sect. 2.2). Little is published about nutrient leaching (Sect. 2.3), and a critical lack of knowledge exists on the interplay of these three key ecological aspects. The net effects of (winter) climate change on the C cycle, i.e., the biotic feedback to climate change, can therefore hardly be assessed up to now (Sect. 3).

2.1 *Primary Production*

The general expectation of increased primary production with warming is used to explain the greening or “shrubbification” of the Arctic over the past decades (Elmendorf et al. 2012). This expectation appears sound as temperate, boreal, and arctic plant species are clearly temperature-limited over winter (Larcher 2003) and as elongation of the growing season increases primary production (Slayback et al. 2003). Furthermore, there is experimental evidence that increased snow depth enhances plant growth of arctic shrubs (Krab et al. 2018). However, the recently described “arctic browning” (Phoenix and Bjerke 2016) warns against naïve extrapolation of the “greening” trend. Increased fire frequency (Bret-Harte et al. 2013) or pest outbreaks (Netherer and Schopf 2010) are potential explanations for this reversed greening in some regions and at specific times. Winter processes offer other explanations, as increased productivity with longer and warmer growing seasons may be counteracted when (1) winter climate change leads to increased soil freezing, when (2) warmer autumns or warm spells during winter lead to premature dormancy release and increased winter and spring frost damage, when (3) winter warm spells expose plant organs to subsequent frost by melting the insulating snow cover, when (4) winter rain events lead to ice encasement, or when (5) wetter winters delay spring phenology.

1. It is well documented that increased depth and duration of soil freezing caused by snowpack reductions adversely impact root vitality (Comerford et al. 2013; Kreyling et al. 2012a; Reinmann and Templer 2018; Tierney et al. 2001), photosynthesis (Göbel et al. 2019), shoot elongation (Comerford et al. 2013), and N uptake by trees (Campbell et al. 2014). Root frost damage can even lead to regional dieback of ecologically and economically important tree species, as the example of *Chamaecyparis nootkatensis* (yellow cedar) in the Pacific Northwest implies (Schaberg et al. 2008; Buma et al. 2017). For the cold-temperate regions where soil frost is expected to increase in frequency and magnitude due to reduced snow cover, growth and C sequestration in the deciduous forests might be most adversely impacted by this projected shift in winter climate (Reinmann et al. 2019). Here, reduced stem growth might be explained as a passive consequence of reduced nutrient availability. Alternatively and more likely in light of the below described increase in nutrient availability (Sect. 2.2) with soil frost, C resources might be actively shifted belowground to facilitate compensatory root growth later in the year, which is a common consequence of increased root damage due to soil frost (Gaul et al. 2008; Sorensen et al. 2016). Studies on root-stem resource allocation (e.g., studies on within-tree dynamics of nonstructural carbohydrates (Hartmann and Trumbore 2016)) that could distinguish between these two alternative mechanistic explanations are so far lacking.

   Changes in the frequency of soil frost events, i.e., the number of freeze-thaw cycles, are another aspect of altered winter insulation of soils, yet they appear to only have minor or transient effects on plant performance (Kreyling et al. 2010, 2012b; Larsen et al. 2007). Taken together, lethal and sublethal root and shoot damage are expected to slow down or even reverse the projected increase in primary productivity in regions with increased incidence of soil frost events due to permanently or temporarily reduced snow cover.
2. Temperate species can incur freezing damage at temperatures in the range of −5 to −10°C but survive much colder temperatures in winter after successful hardening in a dormant state (Noshiro and Sakai 1979). With climate change, plants may be particularly vulnerable to frost in late winter and early spring because of premature dehardening (Augspurger 2013; Gu et al. 2008; Rigby and Porporato 2008; Liu et al. 2018; Montwé et al. 2018). Such premature dehardening can be caused by several interrelated effects such as cold acclimation occurring later in autumn, under shorter photoperiod and lower light intensity, all affecting the energy partitioning between growth, built-up of reserves, and cold acclimation that can further be influenced by elevated atmospheric CO_2 concentrations (Rapacz et al. 2014). Temperate deciduous tree species differ considerably in budburst forcing requirements and photoperiod sensitivity (Malyshev et al. 2018) and, consequently, in winter (Kreyling et al. 2015a) and

spring (Muffler et al. 2016) frost tolerance, indicating that winter climate changes also have the potential to affect competitive balances between co-occurring species. Generally, spring damage is potentially more relevant than winter damage because woody species have the ability to adjust winter frost tolerance to ambient conditions dynamically, while frost tolerance around budburst is minimal and nonadaptable (Vitra et al. 2017). Midwinter warming events, however, can break dormancy in temperate (Kreyling et al. 2015b), boreal (Ogren 1996), and arctic (Bokhorst et al. 2010b) plants, and early spring warming increases forcing conditions leading to budburst followed by late frost events (Augspurger 2013). Annual wood increment of cool-temperate deciduous trees can be decreased by more than 50% due to single frost events after leaf-out (Príncipe et al. 2017).

Note, though, that winter dormancy is a complex phenomenon as dormancy depth depends not only on forcing temperatures but also on chilling sums, meaning that plants require a certain amount of cold temperatures for dormancy release (Laube et al. 2014). Consequently, warmer winters could also lead to unfulfilled chilling requirements. Until now reported in only one extreme case, winter warming can consequently even lead to strongly delayed spring phenology because of unfulfilled chilling requirements and unbroken dormancy (Yu et al. 2010).

Furthermore, winter temperature and moisture are critical drivers for seed dormancy and germination, and global climate change alters these cues and can compromise seedling emergence and vigor (Walck et al. 2011). Yet, few studies have tested the importance of snow cover and winter temperature on seed survival, germinability, seedling establishment, and growth in response to climate change. First evidence suggests that post-winter seed germination decreases with reduced snow cover in trees that disperse seeds in summer or fall (Drescher and Thomas 2013). Likewise, seed mortality increases with decreasing snow cover over winter for *Fagus crenata* (Homma et al. 1999).

3. Extreme winter warming events leading to snowmelt leave plant shoots vulnerable to cold air temperatures subsequent to the warming event even in arctic ecosystems (Bokhorst et al. 2009, 2011). Again, susceptibility is species-specific, and evergreen plants are more vulnerable than graminoids or deciduous species to such extreme temperature variabilities in the arctic (Bokhorst et al. 2018). Here, subsequent frost damage is not driven by dormancy break but rather by exposing plant organs to frost events which usually are protected by the insulating snow cover. A coordinated distributed experiment at 13 temperate grassland sites implies that negative effects of snow removal on biomass production increase sharply toward colder sites, with up to 25% reduced productivity at cold-temperate sites and no visible effects at cool-temperate sites (Henry et al. 2018). We have further found comparable effects of short-term (2–5 days) winter warming pulses in temperate ecosystems, where at least some species reacted with strongly reduced biomass production, although the increased susceptibility in this case might also be caused by dormancy break (Schuerings et al. 2014).

Observational studies support the findings of these experimental studies: Boreal understory plant species show clear differences in their snow cover preferences (Rasmus et al. 2011), emphasizing the regulatory importance of altered snow cover for species composition. Snow cover manipulations consequently affect species occurrence patterns in boreal (Kreyling et al. 2012a) and, likewise, in steppe (Chi et al. 2018) ecosystems.

4. Ice encasement harms plants by anoxia, accumulation of CO_2, ethanol, lactic acid, and ethylene (Gudleifsson 1994, 2010). More frequent occurrences of rain-on-snow events and midwinter thaw events therefore result in increased damage by ice encasement (Bélanger et al. 2002; Tompkins et al. 2004). However, plants differ in their vulnerability to ice encasement with juvenile conifer trees (Domisch et al. 2018) and alpine plants (Bjerke et al. 2017) reacting quite sensitively, while arctic willow and arctic graminoids appear rather tolerant (Bjerke et al. 2018).

   Extreme aboveground ice encasement furthermore occurs in the form of ice storms, i.e., supercooled rainfall during freezing air temperatures leading to ice coating of aboveground plant organs and, due to the sheer weight, to branch and crown loss of forest trees (Rustad and Campbell 2012). Frequency of such events is projected to increase, at least for the temperate zone of western North America (Cheng et al. 2007).
5. The start date of the growing season can be delayed by increasing winter precipitation (Vaganov et al. 1999). It has recently been shown that extraordinarily wet winters delay the start of the growing season by several days over a wide range of boreal forests due to colder soil temperatures related to both the increase in snowmelt heat flux and reduced absorption of solar radiation, which are proportional to the amount of winter precipitation (Yun et al. 2018).

Taken together, several negative feedbacks to primary production are hidden in projected winter climate changes, and their importance and relative effect sizes are hardly known, in particular in a multi-year perspective. However, evidence suggests the surprising conclusion that we should expect more plant frost damage in a warmer world and that the effects of winter climate change on primary production are not yet studied to a degree that allows for sound predictions into the future.

2.2 Soil Biotic Activity, Litter Decomposition, and Mineralization

Generally, soil warming leads to increased soil biotic activity and mineralization (Rustad et al. 2001). Accordingly, transplanting intact soil cores to warmer sites results in strongly increased nitrogen mineralization with presence or absence of a continuous snow cover mediating this effect (Wang et al. 2016). Zero degrees Celsius represents an important threshold for abrupt changes in microbial activity and substrate usage because of decreasing availability of liquid water (Mikan et al. 2002). However, much colder temperatures are typically required to cause microbial lysis, and microbial growth can continue below freezing (McMahon et al. 2009).

Nevertheless, the sublethal effects of freezing on soil microorganisms are not well understood, and the length of freezing, the number of freeze-thaw cycles, and the rate of freezing can all increase cell damage for a given freezing intensity (Elliott and Henry 2009; Vestgarden and Austnes 2009). In addition, for soil microorganisms that survive freezing and desiccation over winter by accumulating osmolytes, thawing can potentially cause mortality via osmotic shock, caused by exposure to melt water from snow (Jefferies et al. 2010).

Increased snow depth in arctic ecosystems has been shown to decrease richness and lead to a turnover of ectomycorrhizal fungal communities, potentially stimulating C and N mobilization and primary production (Morgado et al. 2016). Increased microbial activity in warmer soils over winter will also increase soil respiration in arctic (Mikan et al. 2002), boreal (Öquist and Laudon 2008), and temperate systems (Muhr et al. 2009; Schuerings et al. 2013). Reduced insulation due to absent snow cover, e.g., after extreme winter warming events, however, can lead to colder soils and strongly reduced annual decomposition rates, as, e.g., shown for a wet boreal forest (Kreyling et al. 2013). Soil microbial biomass, rates of soil C mineralization, and heterotrophic soil respiration in northern temperate hardwood forests, however, do not appear to be altered by reductions in snowpack and increases in soil freezing (Sorensen et al. 2016; Steinweg et al. 2008). Yet, in another snow removal experiment in the same ecosystem, soil respiration increased in response to induced soil frost, probably because of root mortality providing easily decomposable organic matter which might lead to priming and increased SOM degradation (Reinmann and Templer 2018). Infrared warming of a temperate grassland resulted in absence of snow cover, more variable soil temperatures, and unaltered decomposition rates (Walter et al. 2013). Increased soil temperature variability, in particular soil freeze-thaw cycles, adversely affects soil microbial biomass and increases available N and fuel N_2O emissions according to a meta-analysis on 47 available studies (Song et al. 2017). Winter litter decomposition, however, is remarkably unaffected by midwinter warming events leading to snowmelt in arctic ecosystems (Bokhorst et al. 2010a). Methane emissions in response to winter climate change appear less well studied. In an arctic moist tundra, it has been shown that long-term increases in snow accumulation can lead to markedly increased methane emissions, implying a positive feedback to climate warming due to the strong greenhouse capacity of methane (Blanc-Betes et al. 2016).

Taken together, soil warming increases soil biotic activity and litter decomposition. It needs be noted, though, that effect sizes diminish over time (Romero-Olivares et al. 2017). Soil cooling, however, can have various consequences: decreasing soil biotic activity and litter decomposition due to temperature limitation, showing no effect, or even increasing soil biotic activity due to increased supply of easily decomposable necromass. Increased soil temperature variability generally reduces soil biotic biomass but leads to increased soil nutrient availability (Comerford et al. 2013).

2.3 Nutrient Leaching

Increased N leaching following soil freezing has been explained by decreased root uptake due to lethal or sublethal root damage (Campbell et al. 2014; Matzner and Borken 2008). However, the projected increase in winter rain for the temperate regions and in total winter precipitation for arctic regions could further counteract the positive effects of soil warming on tree growth through increased mineralization as the mineralized nutrients might be leached out with the downward flow of the additional water, thereby getting lost for primary production (Bowles et al. 2018). Apart from this general and theoretical expectation, there is surprisingly little literature on this question. Roots occurring in deeper soil layers after winter soil warming have been interpreted as indirect indicator for N leaching (Schuerings et al. 2013). The expectation of increased nutrient leaching might also require fine-tuning to acknowledge potentially negative feedbacks. For instance, the supply of easily decomposable material might decrease with less winter root damage (Tierney et al. 2001) and a reduction in soil aggregate disruption (Oztas and Fayetorbay 2003) for regions with increasing thickness of snow cover and warming soils. Furthermore, despite evidence for increased N leaching losses in response to increased soil frost in some temperate systems (Fitzhugh et al. 2001), the opposite effect has been reported in others (Hentschel et al. 2008). Snow removal leading to colder soils with more frequent freeze-thaw cycles have furthermore been shown to increase ammonium availability but not nitrate loss in a cool-temperate forest in Northern Japan (Shibata et al. 2013). Finally, winter warming pulses can trigger N leaching with plant community composition largely controlling the amount of leaching (Kreyling et al. 2015b).

Overall, responses of soil N retention to winter climate change will depend on the so far understudied balance between plant uptake responses and N leaching losses (Sanders-DeMott et al. 2018), and future projections are hardly possible with the current state of knowledge.

3 Feedbacks from Ecosystems to Climate

Feedbacks in the C cycle between the atmosphere and the terrestrial biosphere remain a considerable source of uncertainty for both global climate projections and predictions of the terrestrial net primary productivity (NPP; Heimann and Reichstein 2008). Empirical studies and the models that rely on them for parameterization often use only growing season climate conditions to explore relationships between climate and plant growth or ecosystem NPP (Friedlingstein et al. 2006; Sanders-DeMott et al. 2017). Concerning northern forest ecosystems (i.e., cold-temperate and boreal forests), satellite data, model projections, and in situ observations imply that C uptake rates have increased due to winter warming that has lengthened the growing season in recent decades (Xia et al. 2014). A decrease in winter snow cover restraining C emissions to the atmosphere due to colder soil temperatures has been shown to cause a negative feedback to global warming for cold-temperate and boreal forests according to Eddy-covariance C flux data (Yu et al. 2016). Still, the strength and temporal variability of such a potential C sink appears uncertain due to potentially confounding effects regulating primary production described above (Sect. 2.1). The large uncertainty in soil C dynamics between multiple models and experiments (Sulman et al. 2018) emphasizes the conclusion that a better understanding of feedbacks between the biosphere and the atmosphere is crucial for both the projections of realized climate change and the ecological impacts of this climate change. Below, I develop hypotheses for biosphere-atmosphere feedbacks which await rigorous testing and point out key uncertainties (summarized in Fig. 3). These hypotheses are based on very simplistic comparisons between trends in C gain through primary production (Sect. 2.1), trends in C loss through decomposition (Sect. 2.2), and potentially limiting effects of increased nutrient leaching (Sect. 2.3) in view of the projected key changes in ecologically relevant climatic parameters (Sect. 1).

3.1 Arctic

Strongly increasing air temperatures lengthen the growing season. Increased snow cover and air warming lead to soil warming. Based on these trends, decomposition and mineralization over winter increase. A shift in the species composition toward more productive species enhances primary production and suppresses nutrient leaching. The net feedback to the climate system depends on relative effect sizes

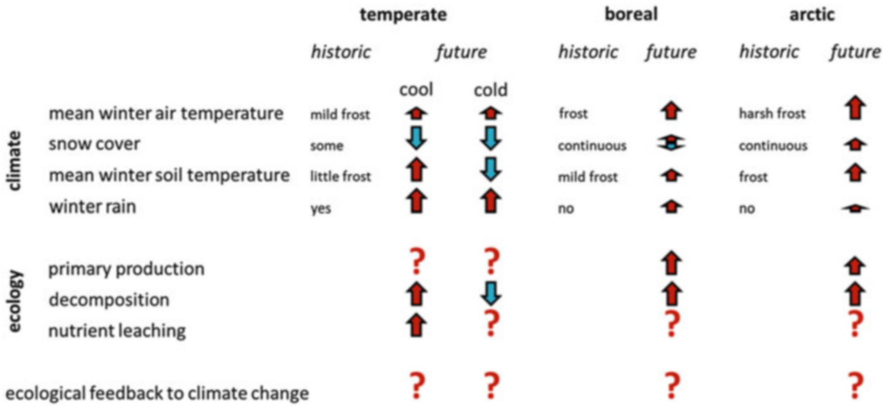

Fig. 3 Winter climate change of ecologically relevant parameters, their hypothetical effects on ecosystem functioning, and potential feedbacks to the climate systems separated by biomes

of increased decomposition in comparison to increased production, with the latter being complicated by several potentially negative balances such as increased climatic variability resulting in more frequent midwinter melting and rain-on-snow events which damage plant organs and can lead to dieback. The role of winter climate change on the net feedback of the biosphere to climate change is currently unclear for arctic ecosystems.

3.2 Boreal

Increasing air temperatures lengthen the growing season. Together with slightly increased or unaltered snow cover, air warming leads to slight soil warming. Based on these trends, decomposition and mineralization increase. Primary production increases. Nutrient leaching increases mainly during extreme events which limit primary production, e.g., due to increased climatic variability resulting in more frequent midwinter melting or rain-on-snow events which damage plant organs and can lead to plant dieback. Plant community composition is altered by these winter climate changes; its feedback on decomposition and nutrient leaching is unclear. The role of winter climate change on the net feedback of the biosphere to climate change is currently unclear for boreal ecosystems.

3.3 Temperate

Temperate ecosystems move toward opposing winter climate regimes. Cold-temperate ecosystems are influenced by the apparent paradox of “colder soils in a warmer world” (Groffman et al. 2001) due to air temperatures still being cold while soils being no longer protected by an insulating snow cover. This leads to reduced decomposition rates over winter and reduced primary production due to (sub)lethal root damage which further allows for increased nutrient leaching. Primary production is further limited by more frost damage to aboveground plant organs because of reduced frost tolerance and earlier leaf-out despite increased climatic variability leading to damaging frost events mainly in spring.

Cool-temperate systems are no longer snow-covered and air warming exceeds the cooling capacity of a missing snow cover for soil temperature. Consequently, air and soil temperatures increase, lengthening the growing season, increasing primary production and increasing decomposition rates. Markedly more winter rainfall, however, leads to nutrient leaching which limits primary production. Effect sizes here are unknown. Primary production is further limited by more frost damage to aboveground plant organs because of reduced frost tolerance and earlier leaf-out despite increased climatic variability leading to damaging frost events mainly in spring.

The role of winter climate change on the net feedback of the biosphere to climate change is currently unclear for temperate ecosystems.

4 Summary and Key Uncertainties

Up to now, winter climate change effects on key ecological processes, i.e., primary production, decomposition, and nutrient leaching, are understudied in temperate, boreal, and arctic ecosystems. Surprisingly, uncertainties even about directions of change are largest for cold-temperate ecosystems. Change in snow cover and its effect on soil temperatures have been identified as key aspect in winter climate change. Clearly, better projections of soil temperature and climatic variability are needed from climate models in order to better predict ecological feedback loops to climate change and inform experiments about realistic manipulations (see Fig. 4 for potential experimental designs). Generally, experimental and observational studies need to shed light on temporal hierarchies in ecological processes, such as the role of root damage and root activity for decomposition of soil organic matter ("priming"; Kuzyakov 2010) or shifts in plant species composition due to winter climate change determining primary production (Krab et al. 2018) as well as litter quantity and decomposability (Cornelissen et al. 2007). Primary production is furthermore strongly determined by phenology, and a sound understanding of changes in the growing season needs to acknowledge not only the obvious but also the "hidden" aspects, i.e., explore the (missing) synchronicity between above- and belowground growth (e.g., Blume-Werry et al. 2016). Another major source of uncertainties are biotic interactions (Makoto et al. 2014) including phenological mismatches (Allstadt et al. 2015) and altered herbivory patterns (Tsunoda et al. 2018). Finally, global change drivers interact and first evidence suggests that this interaction is rarely additive, as shown for instance for the interaction between snow depth changes and N deposition (Vankoughnett and Henry 2014). Evidently, sound projections of future ecosystem functioning and biotic feedbacks to climate change require a comprehensive understanding of winter ecological processes, which have so far been too often neglected.

Fig. 4 Examples for winter climate change manipulation experiments. Top left, soil warming by heating wires in the ground to avoid soil frost come with the drawback that soil warming in the absence of air warming is unrealistic (Schuerings et al. 2013); top right, ecosystem warming by infrared heaters and warming cables on the ground allow for simulation of winter warming extremes as they are able to melt even thick snowpacks quickly (Kreyling et al. 2015b); bottom left, aboveground infrared warming mimics a warmer climate with realistic consequences on snow cover and soil temperature variation (Walter et al. 2013); bottom right, snow-out shelters reduce winter soil insulation while not altering water and nutrient input as the snow accumulated on the top melts through the perforated plastic sheets upon melting events (displayed study unpublished but see Kreyling et al. 2012a for comparable setup). Combining snow-out shelters with realistic changes in winter precipitation amount and/or air temperature warming is a promising approach to test for winter climate change effects in temperate ecosystems

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