

Three decades of environmental change studies at alpine Finse, Norway: climate trends and responses across ecological scales

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Abstract

The International Tundra Experiment (ITEX) was established to understand how environmental change impacts Arctic and alpine ecosystems. The success of the ITEX network has allowed for several important *across-site* syntheses, and for some ITEX sites enough data have now been collected to perform *within-site* syntheses on the effects of environmental change across ecological scales. In this study, we analyze climate data and synthesize three decades of research on the ecological effects of environmental change at the ITEX site at Finse, southern Norway. We found a modest warming rate of +0.36 °C per decade and minor effects on growing season length. Maximum winter snow depth was highest in winters with a positive North Atlantic Oscillation. Our synthesis included 80 ecological studies from Finse, biased towards primary producers with few studies on ecological processes. Species distributions depended on microtopography and microclimate. Experimental warming had contrasting effects on abundance and traits of individual species and only modest effects at the community level above and below ground. In contrast, nutrient addition experiments caused strong responses in primary producer and arthropod communities. This within-site synthesis enabled us to conclude how different environmental changes (experimental and ambient warming, nutrient addition, and environmental gradients) impact across ecological scales, which is challenging to achieve with across-site approaches.

Key words: alpine ecosystems, climate change, experimental manipulation, International Tundra Experiment, open top chamber, within-site synthesis

Introduction

Global climate change affects ecosystems worldwide (Walther et al. 2002), but Arctic and alpine ecosystems are particularly vulnerable, as warming is amplified at high northern latitudes and at high elevations, particularly in winter (Cohen et al. 2014; Stocker 2014; Wang et al. 2016; Qixiang et al. 2018). Climatic changes and subsequent extreme events (Walsh et al. 2020) are coupled to significant responses within the geophysical system; for example, an intensification of the hydrological cycle, permafrost thawing, and decreasing snow cover extent and duration, which in turn can affect biophysical processes as well as species distributions, population dynamics, community composition, and species interactions (Bellard et al. 2012; Box et al. 2019).

The International Tundra Experiment (ITEX; see Henry and Molau 1997) was initiated in 1990 to study the potential responses of Arctic and alpine plant species to predicted

environmental changes in the tundra biome (e.g., Chapin et al. 1991). The network's success is highlighted by a series of synthesis papers documenting such effects, first in a special issue of *Global Change Biology* where several papers reported species' responses to short-term environmental manipulation across ITEX sites, introduced by Henry and Molau (1997). For example, Welker et al. (1997) showed that shoot length, photosynthesis, and biomass of the abundant circumpolar species *Dryas octopetala* L. increased under experimental warming across sites. Subsequently, Arft et al. (1999) demonstrated advanced phenology, a short-term response in vegetative growth, and an increase in reproductive effort in response to warming across 13 ITEX sites. However, these responses differed between functional groups and between High- and Low-Arctic and alpine sites. Several successive studies showed that shrubs increase the most in abundance with warming and that vegetation height increases under

both experimental (Walker et al. 2006; Elmendorf 2012a) and long-term ambient warming (Elmendorf et al. 2012b) negatively affecting the abundance of bryophytes and lichens. While increased height of the plant community was a clear and consistent trait response to warming across 117 tundra sites, responses of other functional traits lagged behind (Bjorkman et al. 2018). By combining data from experimental warming and long-term monitoring efforts, Prév y et al. (2019) found that the flowering season contracts as late flowering plants show stronger phenological responses than early flowering species. Although these studies differ in their approaches, e.g., utilizing plot-scale observations (Elmendorf et al. 2012b), responses to in situ manipulations (Elmendorf et al. 2012a), or compare monitoring, manipulation, and space-for-time approaches simultaneously (Elmendorf et al. 2015; Pr v y et al. 2019), they have in common that they synthesize the responses to environmental change within trophic levels, across sites.

At many study sites, including ITEX sites, field experiments have been maintained for several decades, and a large amount of data on various components of the local ecosystem has accumulated. As such, researchers and their students concentrate their ecological research at specific sites and subsequently build long-term data series. Therefore, we argue that the time is ripe for within-site syntheses of available data, which will increase our understanding of ecosystem responses to environmental change across ecological scales. Such endeavors are relatively novel, but one synthesis of 18 years of ecological monitoring on Herschel Island (Qikiqtaruk), Canada, revealed an increase in growing season length, advanced phenology, taller vegetation, and changes in plant community composition (Myers-Smith et al. 2019). Depending on the data available, within-site reviews can help to disentangle species versus community-level responses to environmental change and responses to ambient versus experimental environmental changes. Further, they can help clarify interactions across trophic levels and allow for comparisons between taxonomy- and trait-based approaches. Finally, they can put the studies at the individual sites into context with the broader, biome-wide syntheses.

In this study, we synthesize nearly three decades of observational and experimental ecological research performed at or near the alpine ITEX site at Finse, southern Norway. The main site is located at Mt. Sanddalsnuten (approximately 1500 m a.s.l.), but we include work from several subsites located near Finse between approximately 1200 and 1500 m a.s.l. We first assess how the climate at Finse has changed over the past three decades in terms of temperature, growing season length, the frequency of frost during the growing season, and how local snow conditions have changed. Further, we summarize existing knowledge on species distributions across gradients in elevation, microtopography, and microclimate. Subsequently, we synthesize how alpine species respond to environmental change in terms of their abundance, functional traits, life history, and phenology. We then describe how the responses of individual species could translate into altered community composition, diversity, and species interactions. Finally, we discuss how altered species interactions and traits at the community level may translate into

altered ecosystem processes. This synthesis illustrates the important insights that can be acquired from the collective research performed at one site and serves as a basis to further substantiate our understanding of climate change effects on the alpine ecosystem.

Methodology

Site description

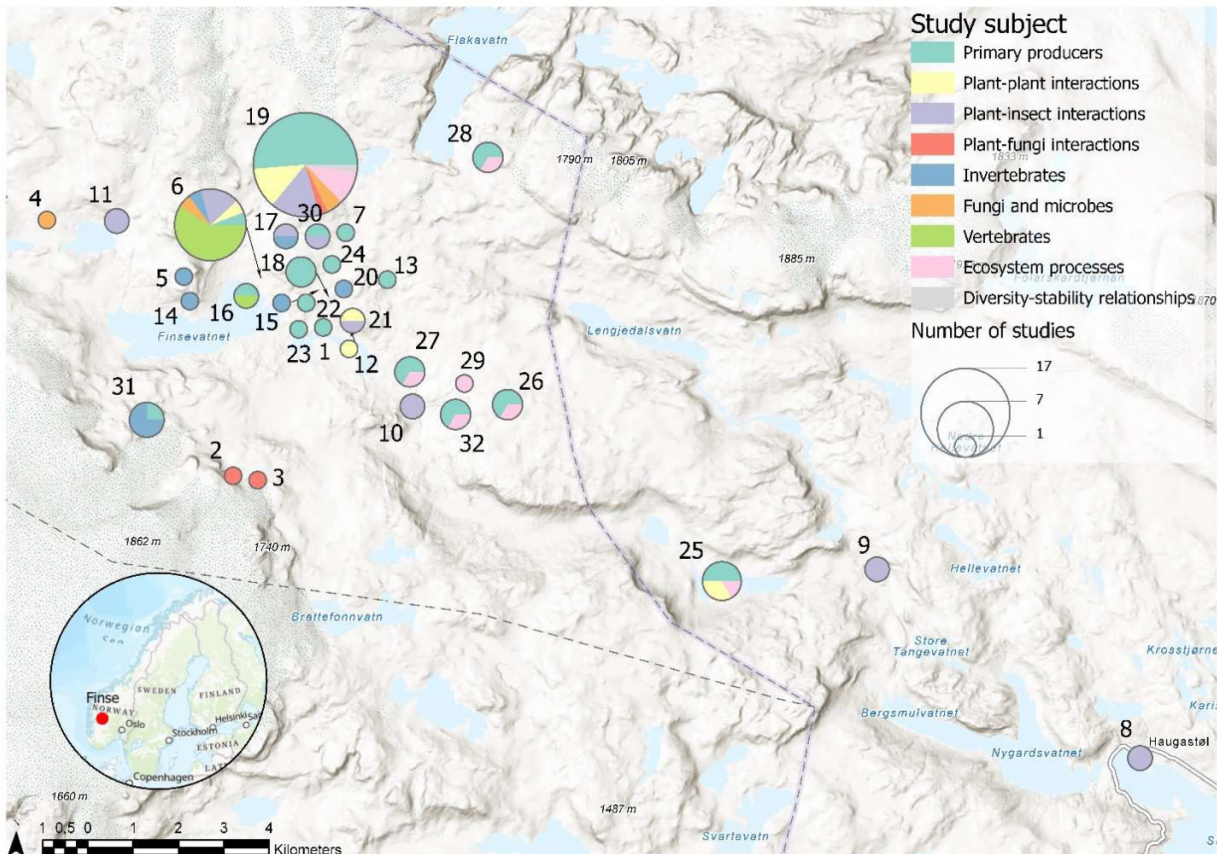
The main ITEX site at Finse (60.626°N; 7.522°E, at approximately 1500 m a.s.l.) is located near the peak of Mt. Sanddalsnuten (1554 m a.s.l.) in the Scandes mountains of southern Norway, within the 450 km² Hallingskarvet National Park. Due to its calcareous phyllite bedrock that contrasts the acidic granite more common in the Finse valley (Dahl 1997; Askvik 2008), the ITEX site at Sanddalsnuten supports a species-rich alpine heath community dominated by *D. octopetala*. In this synthesis, we include studies from several additional research sites near Finse, including snow fields on the lee sides of Sanddalsnuten (i.e., aspects between east and north) and the valley towards Jomfrunuten (1471 m a.s.l.) where biological soil crusts, bryophytes, graminoids, *Salix herbacea* L., and forbs such as *Ranunculus acris* L. are common. Locations of the studies included in this synthesis can be found in Fig. 1.

Climate data and analyses

Climate and weather data from Finse

Daily minimum, maximum, and average temperatures at 2 m above ground level, as well as daily maximum snow depth and monthly temperature and precipitation data used in this study, are publicly available through the Norwegian Meteorological office's climate databases *Seklima.no* (2020a) and *SeNorge.no* (2020). The monthly data were available to June 2020, and the daily data were available to August 2020 at the time of analysis. The data originate from two different weather stations near Finse, jointly operated by the Norwegian Meteorological office and the Finse Alpine Research Center. The first, named Finse (SN25840, WMO: 1351), was located at 1223 m a.s.l. (60.603°N; 7.504°E) and was active from November 1, 1969, to June 29, 1994. The second station, Finsevatn (SN25830, WMO: 1350), has been active from May 1, 2002, to the present (1210 m a.s.l., 60.594°N; 7.527°E). Consequently, a gap in the climate data exists between July 1994 and April 2002. In addition, smaller gaps in the data exist due to equipment failure, and these are summarized in Supplementary Table S1. The new weather station (Finsevatn) was established approximately 1.6 km southeast of the old weather station (Finse). The Finse station was located in a snow bed, while the Finsevatn station is located on a wind-exposed ridge. Because of these differences between the two stations, analyses based on daily maximum, minimum, and average temperatures were performed for each of the stations separately. In contrast, analyses based on monthly temperature and precipitation included data from both stations, as we consider local differences in microclimate to average out on a monthly timescale. Snow depth data were collected daily

Fig. 1. Map of the Finse area showing the sites of the 80 studies included in this synthesis. Each unique study location is indicated with a number, which refers to Supplementary Table S1. One central coordinate was used for studies that included multiple sites close to each other. Location 6 includes the studies that do not refer to any specific study site, and location 19 refers to the main ITEX site at Mt. Sanddalsnuten. The circle size (surface area) of each pie chart is relative to the number of studies performed at each site, while the colors indicate the relative representation of study topics. The map was created with ArcGIS Pro v2.5.0 (Esri 2020) using a standard background map.



from 1969 to 1994 at the Finse station at 8 am by an observer. Unfortunately, no data on snow depth were available for the Finsevatn weather station between its establishment in May 2002 and 2017. Because the data series at Finsevatn would consist only of 4 years (i.e., 2017–2020) and the two weather stations are at locations with different snow dynamics, only snow depth data from the Finse station were analyzed. Information about the weather stations and the data they record can be found at the station overview of the Norwegian Meteorological office at [SeKlima.no](https://seklima.no) (2020b).

Annual and seasonal temperature trends

To calculate decadal trends in annual and seasonal temperatures, we used monthly average 2 m temperature data from both weather stations. All missing monthly values (Supplementary Table S1) were substituted with interpolated monthly average temperatures provided by the Norwegian Meteorological office (MetNorge 2020). The substituted data consisted of interpolated daily mean temperatures for the 1 × 1 km grid cell closest to Finse, based on values recorded at nearby weather stations and interpolated using a Bayesian

optimal interpolation method that incorporates the effects of elevation (Lussana et al. 2018). From these interpolated daily average temperatures, monthly means were calculated. Interpolated monthly temperatures correlated strongly with those observed at both weather stations (R^2 of 0.997 for Finse and 0.995 for Finsevatn, respectively; see Supplementary Figure S1). Winter was defined as December through February, spring as March through May, summer as June through August, and autumn as September through November. To test for decadal trends, we performed simple linear regression analyses in R version 4.0.0 (R Core Team 2020).

Growing seasons, growing degree days, and frost days

We calculated the approximate growing season start, end, and length based on daily 2 m average temperatures from the two weather stations at Finse. In the alpine, the growing season starts as soon as the snow melts. To calculate the length and accumulated warmth of the snow-free growing season, we use two different temperature thresholds: a daily average of 5 and 0 °C. As such, 5 °C is a common threshold used to

define plant growth (Maxwell 1992) but is likely a conservative estimate for the growing season in the Arctic and alpine. On the other hand, the 0 °C threshold may be an optimistic estimate, as snow can persist while daily average temperatures have risen above freezing. Specifically, the start of a season was defined as the first day of the first block of at least 5 days above the threshold temperature, and the end as the last day in the last block of at least 5 days above the threshold, for each year. To exclude warm periods in mid-winter, the 5 °C growing season was calculated between day of year (DOY) 91 and 304 and the 0 °C growing season between DOY 60 and 334. Years missing more than 10 days of average temperature data during these periods were excluded from further analyses (year 1969, 1982, 1991, 1994 through 2004, and 2012). For any remaining days with missing average temperature data (i.e., for years with less than 10 days with missing data), the daily average temperature was calculated as the average (Tavg) of the daily minimum and maximum temperatures on that day (for 43 days in the data set). Subsequently, we calculated accumulated thawing degree days (TDD) using the 0 °C threshold (Tbase) and accumulated growing degree days (GDD) using the 5 °C threshold. TDD was thus calculated as

$$\sum_{i=60}^{334} \text{GDU}_{\text{Tbase}=0\text{ }^{\circ}\text{C}, i}$$

and GDD as

$$\sum_{i=91}^{304} \text{GDU}_{\text{Tbase}=5\text{ }^{\circ}\text{C}, i}$$

where growing degree unit (GDU) = max(Tavg – Tbase, 0). Finally, we calculated the number of frost days (minimum daily temperature below 0 °C) during the 5 °C growing season and 0 °C growing season for each year. In this analysis, seasons missing more than 10 days of minimum temperatures were excluded from analysis. To test for temporal trends, we performed simple linear regression analyses in R version 4.0.0. Separate analyses were performed for each of the weather stations as no interpolated data were used for daily values to fill the 1994–2002 data gap.

Snow and its relation to North Atlantic Oscillation

The reported average yearly precipitation for Finse is 1030 mm over 1969–1990 (Førland 1993), and we found no significant trend over time in total annual precipitation over 1969–2020 (estimate = –18 mm decade⁻¹, R² = 0.02, *p* = 0.423; Supplementary Figure S2). In winter, precipitation falls as snow, and the landscape is typically snow-covered from November to May, but in some years snow can persist through summer across substantial parts of the landscape (R.E. Roos 2020, personal observations). In our analyses, we use snow depth data from the Finse weather station (i.e., winter 1970–1994). We then used a simple linear model in R version 4.0.0 to test for trends in maximum snow cover over time. Further, to explore how local snow conditions relate to, and can possibly be predicted by, large-scale atmospheric

circulation patterns, we extracted winter (December–March) North Atlantic Oscillation (NAO) indices (principal component based) sensu Hurrell and Deser (2010) from the Climate Data Guide database (NCAR 2020) and correlated these to the maximum daily observed snow depth (December–March) at the Finse weather station (1970–1994). A positive NAO phase indicates a zonal flow pattern with low pressure around Iceland in combination with a strong Azores High and thus the dominating Westerlies over NW Europe. In contrast, a negative NAO phase corresponds to more meridional flow over the North Atlantic and thus reduced westerly flows and greater frequencies of dry and easterly weather patterns in NW Europe (Hurrell 1995). To test for any differences in maximum snow depth between winters with an overall positive versus those dominated by a negative NAO pattern, we used a Wilcoxon rank sum test with continuity correction in R version 4.0.0. To test whether deep snow cover translates to late snow melt out, we correlate maximum winter snow depth with snow melt-out date (the first day of the year without snow depth recorded). Years with missing data (1976 through 1980, 1992, and 1994), and those with an unrealistic drop in snow depth, i.e., a snow-free day succeeding a day with >50 cm snow depth (1970 and 1972), were excluded from analyses.

Literature synthesis

Our synthesis of ecological responses to environmental change at Finse is based on previously published literature. To find relevant literature, we performed a search in ISI Web of Science using the search criteria “Title: (Sand?alsnuten OR Finse) OR Topic: (Sand?alsnuten OR Finse)”, which revealed 56 hits (September 2020). Because ISI Web of Science and other literature databases known to us do not allow searches within the methodology sections of articles or searches on geographical locations, we performed searches in additional databases such as Google Scholar (“Finse” and “Sanddalsnuten”) and the library at the Finse Alpine Research Center. Because several studies known to us were not included in the results of the database searches, we further extended our selection by screening reference lists in selected literature and knowledge of studies and authors through our own work. Studies were eligible for inclusion in this review if their focus was on terrestrial ecology at or near the ITEX site at Sanddalsnuten or Finse and were relevant to understand ecological responses to environmental change. As such, studies primarily focused on aquatic systems (e.g., rivers and lakes) were not included. Moreover, studies in geology, glaciology, and physics were only included if they were ecologically relevant. To plot the study locations on the map (Fig. 1), we used ArcGIS Pro v2.5.0 (Esri 2020).

Results

Environmental change at Finse

Annual and seasonal temperature trends

The average annual temperature at Finse measured over 1970–1990 was –2.0 °C and increased by 0.36 °C per decade

over the period 1970–2020 ($R^2 = 0.322$, $p < 0.001$) based on data from both the Finse and Finsevatn weather station, as well as interpolated data. Spring (average -4.0 °C) and summer ($+6.4$ °C) showed trends of $+0.29$ °C ($R^2 = 0.144$, $p = 0.006$) and $+0.34$ °C per decade ($R^2 = 0.192$, $p = 0.001$), respectively. Autumn (average -1.2 °C) showed a more pronounced trend of $+0.45$ °C per decade ($R^2 = 0.247$, $p < 0.001$). For winter (average -9.1 °C), the decadal trend ($+0.38$ °C per decade) was not significant (Fig. 2).

Growing seasons, growing degree days, and frost days

The average length of the 0 °C growing season was 162 days for Finse (1970–1993) and 175 days for Finsevatn (2005–2020), while the 5 °C growing season was 83 and 97 days, respectively. The start of the 0 °C growing season advanced with 0.89 days per year ($R^2 = 0.327$, $p = 0.007$) over the period 1970–1993, and the length of this season therefore also increased with 1.0 day per year ($R^2 = 0.199$, $p = 0.043$; Figs. 3a and 3b). Other growing season parameters showed non-significant trends only (Supplementary Table S2). The average TDD at Finse (1970–1993) was 763, and the average accumulated GDD was 196, while for Finsevatn (2005–2020) 977 TDD and 316 GDD were accumulated annually. At Finse (1970–1993) there was a non-significant negative trend in accumulated TDD and GDD, while for Finsevatn (2005–2020) TDD showed a non-significant increase over time (Fig. 3c; Supplementary Table S2). The occurrence of frost during the growing season showed a positive but a non-significant trend over time for both time periods, most notably during the 0 °C growing season (Fig. 3d; Supplementary Table S2).

Snow dynamics

Maximum winter snow depth (1970–1994) varied between 120 cm (1977) and 425 cm (1976), without a significant linear trend through time (estimate = 3.825, $R^2 = 0.07$, $p = 0.222$). For the 16 years where snow depth data were available until the snow had completely melted, maximum snow depth was positively correlated with snow melt-out date (slope = $+0.14$ d cm^{-1} , $R^2 = 0.48$, $p = 0.004$). The maximum winter snow depth observed at the Finse weather station was 2.28 times greater (365 cm versus 160 cm, respectively) in years with a positive NAO (dominating westerlies) compared to years with a negative NAO ($W = 0$, p -value < 0.001 ; Fig. 4b). In addition, positive NAO winters tended to be milder (Fig. 4a), although cold winters with high maximum snow depth have also occurred.

Ecological responses to environmental change at Finse

Our literature search resulted in a total of 80 studies on ecological responses to environmental change at Finse between 1975 and 2022 (Supplementary Table S3 and Fig. 5). Most studies focused on plants (both vascular and non-vascular) and lichens (35) and how they interact with insects (nine studies), each other (seven studies), or fungi (three studies) while

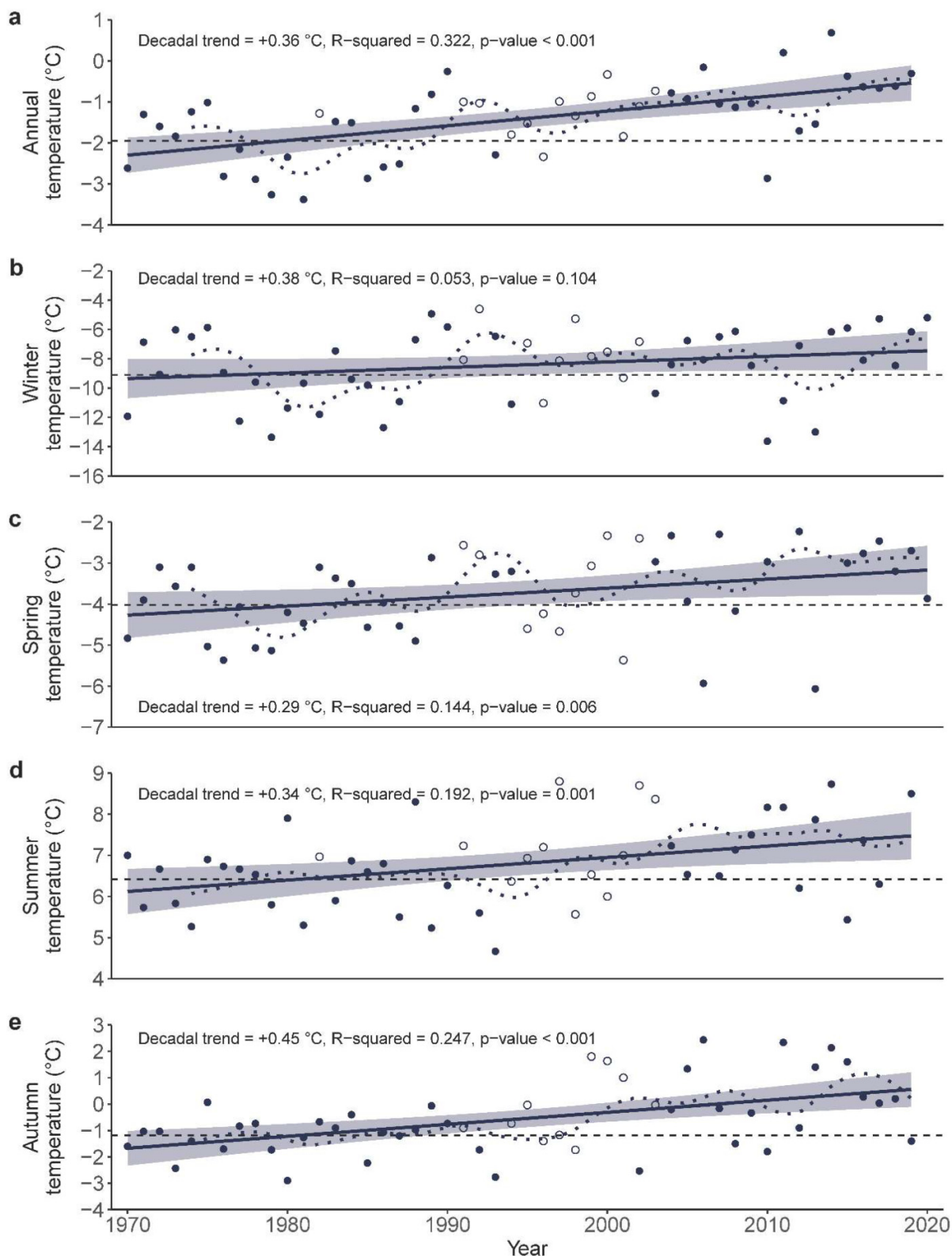
only six studies focused specifically on ecosystem processes such as decomposition and nutrient cycling (Fig. 5). These studies include a variety of experimental approaches, such as environmental manipulations (warming by open top chambers (OTCs) and (or) nutrient additions (28 studies), environmental and successional gradients (21 and 7 studies, respectively), and manipulation of community composition (four studies) or individuals (two studies). In the following sections, we first present how microclimate and topography affect the distribution of primary producers (including vascular plants, lichens, and bryophytes), arthropods, and vertebrates. Then, we address the results from studies on how environmental change affects the populations, traits, reproduction, and phenology of individual species. Finally, we report the effects of environmental change on taxonomic and functional community composition, species interactions, and ecosystem processes.

Landscape heterogeneity and microclimatic drivers of species distributions

The landscape at Finse is heterogenous, and (micro)climatic gradients drive the distribution of species across the landscape. As such, several studies found that soil conditions and timing of snow melt explain the distribution of vegetation types (Heegaard 2002; Reinhardt and Odland 2012; Reinhardt et al. 2013). In addition, the richness of vascular plants and bryophytes at Finse is mostly driven by gradients in soil nutrients, snow duration, and light availability, but these drivers are often correlated and can be challenging to disentangle (Odland et al. 2015). Further, Opedal et al. (2015) found that topographically rough (and thus microclimatically more diverse) sites supported greater vascular plant species numbers as well as a higher beta diversity than flat sites. Snow accumulates in depressions in the landscape, while wind-exposed ridges feature thin snow cover throughout winter. Different lichen species are adapted to these different snow conditions and transplanting lichens away from their native microclimate, adversely affected their growth rates and survival after one winter (Bidussi et al. 2016). We know little about the distribution and microclimatic preferences of fungi despite their high abundance and diversity at Finse (Gulden 1980; Noordeloos and Gulden 1989) and symbioses with alpine plants (Blaalid et al. 2012; Davey et al. 2015).

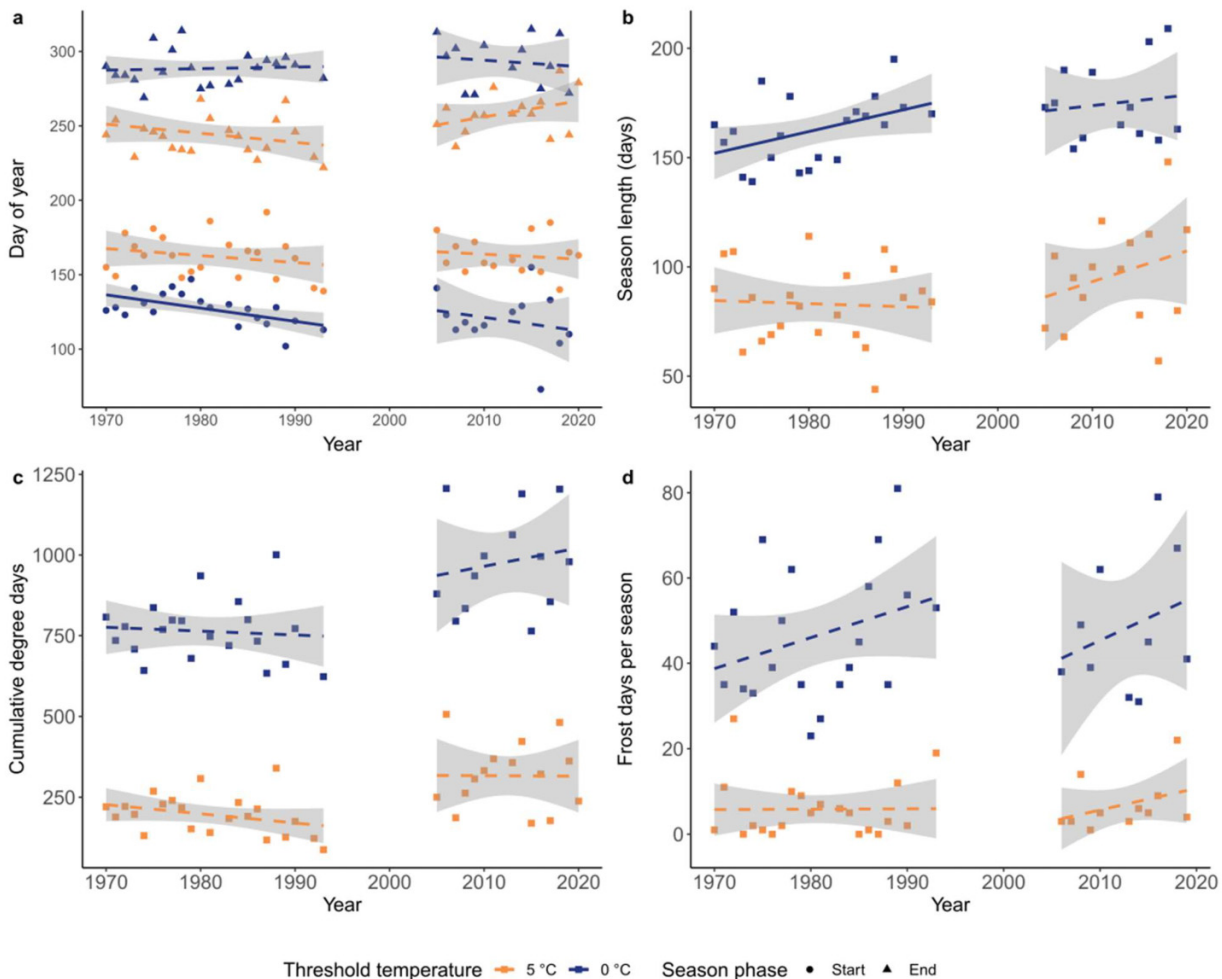
Microclimatic conditions also drive the distribution of non-sessile organisms at Finse. Although some arthropods, such as oribatid mites that live on rocks, showed remarkable tolerances to drought and extreme cold (Sjursen and Sømme 2000), different arthropod species occupied separate niches across variation in soil moisture and show contrasting temporal activity patterns (Ottesen 1996). The distribution of spider species was related to microclimatic conditions such as temperature, moisture, and soil nutrient availability (Hauge and Ottesen 2002). As such, climatically “mild” sites were dominated by lowland spider species, whereas alpine species were common in “severe” (both dry and cold as well as wet and cold) sites. In the low alpine zone where *Salix* shrubs form dense stands, lowland forest spider species were relatively

Fig. 2. Time series of annual (a); winter: December–February (b); spring: March–May (c); summer: June–August (d); and autumn: September–November (e) temperatures at the Finse (1969–1994) and Finsevatn (2003–2020) weather station. Annual and seasonal temperatures where at least 1 month of interpolated data from the SeNorge database were used are indicated with open circles. Closed circles indicate that data are entirely based on station observations. Dashed lines indicate the 1970–1990 average for the respective season, while dotted lines show a smoothed 5-year rolling average. Trendlines (solid) were calculated from a simple linear model, and shaded areas indicate a 95% CI. Note that y-axis scales differ between panels.



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Fig. 3. Day of the year when the growing season starts (circles) and ends (triangles), using a 0 °C (blue) and 5 °C (orange) threshold to define the growing season (a). The length of the 0 and 5 °C growing season in days (b). Accumulated thawing degree days (heat sum with 0 °C base temperature) and growing degree days (heat sum with 5 °C base temperature) (c). The number of days with minimum temperatures below freezing point during the 0 and 5 °C growing seasons (d). Data were calculated from daily temperature (2 m), measured at the Finse (1970–1994) and Finsevatn (2003–present) weather stations. Shaded areas indicate 95% confidence intervals. Solid lines denote significant trends ($p < 0.05$).



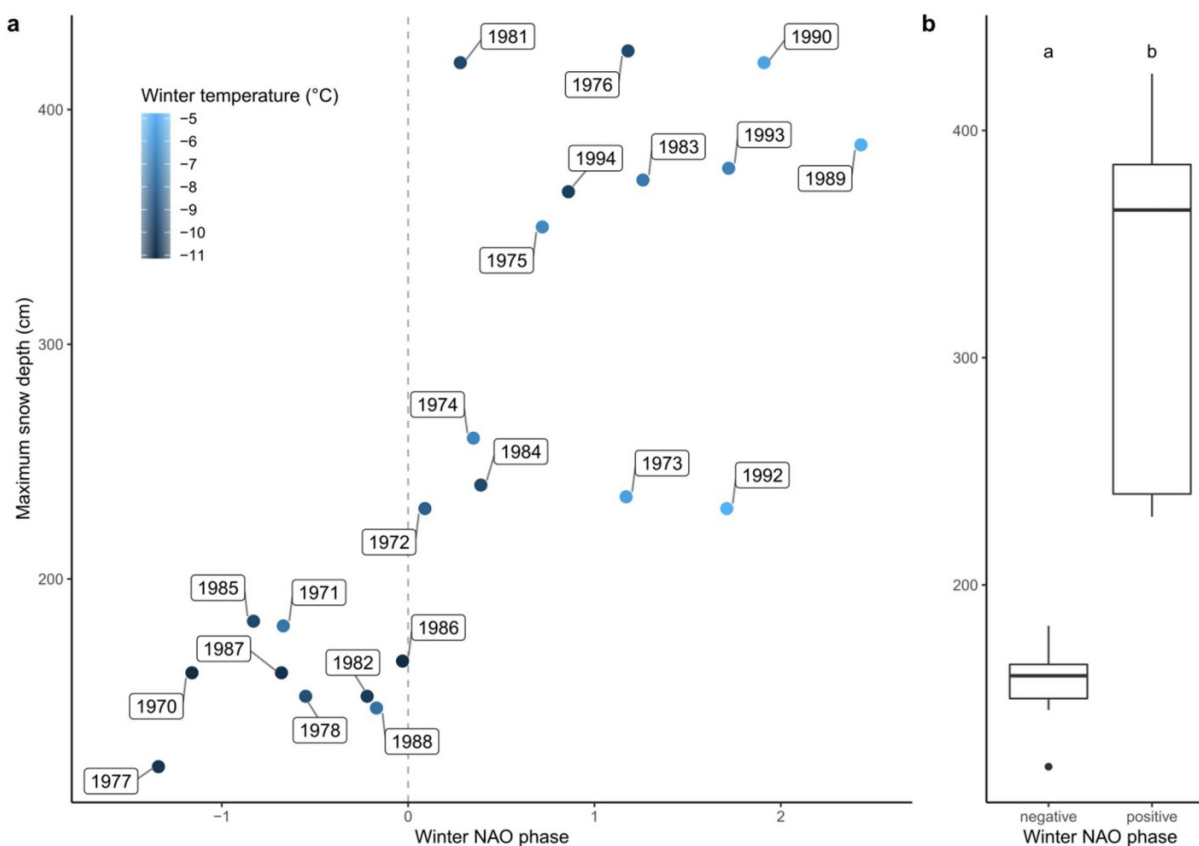
common (Hauge and Ottesen 2002). Closely related arthropod species whose distribution correlates with the distribution of their host plants (e.g., Psyllidae on *Salix lapponum* L.) were separated across elevation gradients through thermal requirements and phenological synchronization with the host plant (Hill and Hodkinson 1995; Hill et al. 1998).

The glaciers at Finse, including the large Hardangerjøkulen, are retreating (Giesen and Oerlemans 2010), and, as the ice melts, new parts of the landscape open up for colonization. Paradoxically, consumers such as Collembola, Oribatida, and Coleoptera are often the first organisms to colonize glacial forelands as establishment is generally more limiting than dispersion (e.g., Bråten et al. 2012; Hågvær 2012; Flø and Hågvær 2013). Previously, it was assumed that these consumers feed on blown-in plant material and prey animals, but, at Finse, Hågvær and Ohlson (2013) showed that both aquatic and terrestrial arthropod pioneer communities (e.g., Coleoptera, Araneae) ate locally derived midges that

contained ancient carbon released from the glacier. These findings suggest that the pioneer food chain is based on “old” carbon and challenges the idea that glacial forelands are examples of primary succession uninfluenced by resources from previous ecosystems.

Finse features populations of mammals such as rodents (e.g., voles and lemming), mountain hare, wild reindeer, and domestic sheep. Although their population dynamics extend across a spatial scale that is beyond the scope of this site-specific synthesis, the ecology of several mammal species impacts the vegetation and soil and is thus relevant to species interactions and ecosystem dynamics at the Finse ITEX site. For example, rodents can affect vegetation by grazing and burrowing (e.g., from nearby Dovrefjell; Nystuen et al. 2014), which has been shown on one particular plant species at Finse, the annual *Euphrasia frigida* Pugsley. For this species, population densities were highest at intermediate levels of rodent disturbance (Nylén and Totland 1999). Voles

Fig. 4. Maximum recorded snow depth at the Finse weather station (1970–1994) versus winter (December–March) North Atlantic Oscillation (NAO) index (a). Colors denote average temperatures over the same period. Winters with a predominantly positive NAO phase accumulate a significantly deeper snowpack (b).



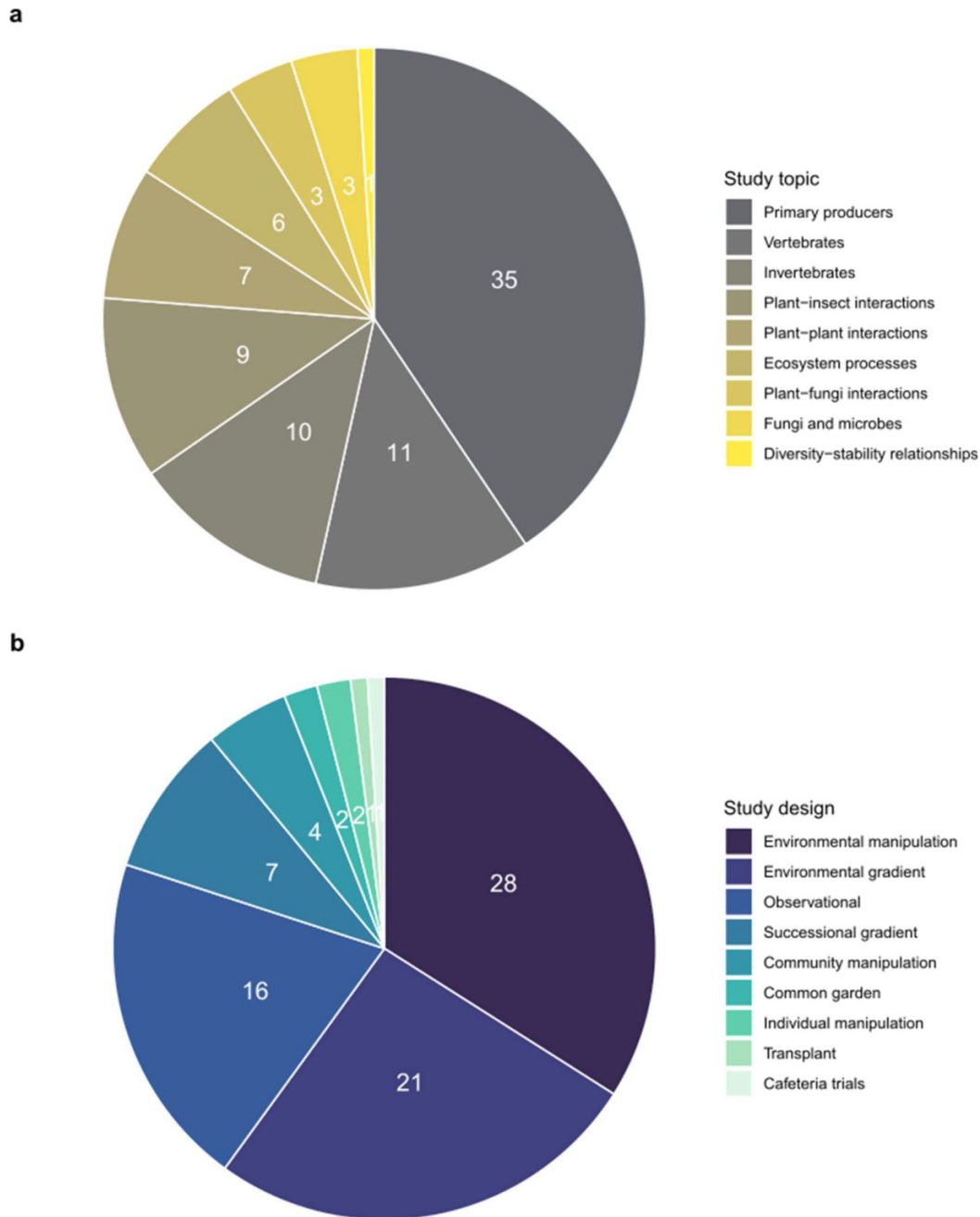
(*Microtus* spp.) and lemming (*Lemmus lemmus* (Linnaeus, 1758)) show classic peaks in population densities but do so less frequently at Finse than in other areas in Fennoscandia (Framstad 2020). Although their population cycles are most often portrayed as density dependent or driven by predator–prey interactions (Steen et al. 1997; Stenseth et al. 1998), lemming populations at Finse and Hardangervidda may be driven by the availability of food, notably bryophytes (Turchin et al. 2000), plant defense chemicals (Seldal et al. 1994), and (changes in) winter weather and snow conditions (Kausrud et al. 2008; Landa 2020). Other important grazers in the area are mountain hare (*Lepus timidus* (Linnaeus, 1758)), domestic sheep (*Ovis aries* (Linnaeus, 1758)), and wild reindeer (*Rangifer tarandus* ssp. *tarandus* (Linnaeus, 1758)). Mountain hares exploit a wide variety of plants as food but preferred forbs (Johannessen and Samset 1994). While reindeer and domestic sheep overlap considerably in dietary preferences (in summer), their spatial distributions rarely overlap (Skogland 1984), and sheep are brought to farms at lower elevation in winter. In fact, reindeer avoid the Finse area due to high tourist densities and human infrastructure such as the railway (Gundersen et al. 2019). It is therefore likely that their impact on the vegetation at the ITEX site is minor compared to that of domestic sheep, which visit frequently. Large mammalian predators have been absent from the Finse area in recent times, but Arctic fox (*Vulpes lagopus*

(Linnaeus, 1758), Landa et al. 2017) and the invasive American mink (*Neovison vison* (Schreber, 1777)) do occur (Hagelin 2016). The complete faunal structure of Hardangervidda, including Finse, was summarized in detail by Solhøy et al. (1975).

Species-specific responses to environmental change

The changes in population density of alpine plant species in response to experimental warming (by OTCs) and nutrient addition were strongly species specific, both after 4 years within *Dryas* heath (Klanderud 2008) and after 5 years in snowbed communities (Sandvik et al. 2004). For example, in the *Dryas* heath, grasses (*Festuca* sp., *Poa alpina* L.) and *Cerastium alpinum* L. increased in abundance in response to experimental warming and nutrient addition, while *Tofieldia pusilla* (Michx.) Pers. decreased. In the snowbed communities, *Salix herbacea* increased in abundance in response to warming while *Carex lachenalii* Schkuhr and *Poa alpina*, among others, did not respond. In many cases, species' responses to warming were amplified by the addition of nutrients (Klanderud 2008). Although the responses of bryophyte and lichen species were more similar in direction (i.e., a decrease in their abundance, particularly when warming and nutrient addition were combined), the magnitude of the responses

Fig. 5. The number of ecological studies (80) performed at Finse per topic (a) and experimental design (b) included in this synthesis. A study can be assigned to multiple topics or experimental designs. Here, *environmental manipulation* includes experiments where temperature, nutrient availability, or other abiotic conditions were altered and compared to control sites. *Environmental gradient* is used in its broadest sense and includes traditional gradients in environment, including elevation, the use of contrasting sites, as well as variations in microclimatic conditions across space or time. *Observational* studies monitor species presence, performance, and behavior in situ, across time and space. *Successional gradient* includes studies performed (across different successional stages) at glacial forelands. In *community manipulations*, one or more species were actively removed or added to an ecological community, while in *individual manipulations* individual organisms were manipulated to investigate their performance. *Transplant* experiments are those where organisms or materials from a common environment are actively transplanted across sites with different environmental conditions. Vice versa, *common garden* comprises those studies where one or more species or materials were moved from their native environments into a common environment. *Cafeteria trials* offer a variety of food items to organisms to establish their dietary preferences.



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varied across individual species (Klanderud 2008). In snow bed habitats, species abundances were already changing under ambient conditions (i.e., the abundances of many of the monitored species were increasing in control plots over the 5 year duration of the experiment) and these changes were amplified by experimental warming for only some herbaceous species (Sandvik et al. 2004). However, due to a general increase in ramet density and the mean abundance per species, which the authors attribute to a potential increase in nutrient availability, a warmer environment may increase the density of snow bed vegetation (Sandvik et al. 2004).

In addition to responses in species' abundance, warming experiments at Finse also affected species' functional traits. For example, experimental warming increased the height of both ridge and leeward vegetation (Nybakken et al. 2011), but the strongest effects on plant size and growth were found when warming was combined with nutrient additions. As such, leaf dry mass of *D. octopetala* increased after 5 years of warming whereas nutrient addition (alone and combined with warming) increased leaf dry weights for *Salix reticulata* L. and *Bistorta vivipara* (L.) Delarbre, both of which did not respond to warming alone (Nybakken et al. 2008). Further, warming did not increase *Saxifraga stellaris* (syn. *Micranthes stellaris* (L.) Galasso, Banfi & Soldano) rosette size (Sandvik and Totland 2000) or the number of leaves of *Thalictrum alpinum* L. and *Carex vaginata* Tausch (Klanderud 2005), but growth and leaf numbers increased in response to nutrient addition or when warming and nutrient addition were combined (Sandvik and Totland 2000). Moreover, the growth of the forb *Parnassia palustris* L. did not respond to experimental warming over 2 years, but warming did positively affect its reproductive traits such as seed number and mass (Sandvik and Eide 2009). The bryophyte *Pohlia wahlenbergii* (F. Weber & D. Mohr) A.L. Andrews showed increased growth (shoot length) after 4 years of warming, and growth further increased when nutrients were also added (Sandvik and Heegaard 2003). In addition, *P. wahlenbergii* adopted a "laxer" growth form with increased temperature or added nutrients, while no significant interaction was found between the treatments. Because a laxer growth form reduces water-holding capacity in bryophytes, such growth responses are only advantageous under continuously moist conditions, such as in snow beds where meltwater is present throughout the entire growing season (Sandvik and Heegaard 2003).

The concentrations of phenolic compounds in individual lichen and plant species were little affected by experimental warming, with a few exceptions (Nybakken et al. 2008, 2011). Although there were no responses of plant tissue C in response to warming, reductions in N concentrations caused C:N ratios to increase for some species. Lichens tended to have lower tissue C under warming, but their C:N ratio was rarely affected (Nybakken et al. 2011; Van Zuijlen et al. 2022b). Similarly, snow bed forbs and sedges showed contrasting responses to long-term (10 year) experimental warming. Specifically, nitrogen concentration decreased in *Cerastium cerastoides* (L.) Britton, *Epilobium anagallidifolium* Lam., and *Carex lachenalii* while C concentrations tended to increase. However, this translated into a significant increase in the C:N ratio for *Cerastium cerastoides* and *Epilobium anagallidifolium*

only (Sandvik and Eide 2011). This indicates a potential dilution effect where increases in C uptake by photosynthesis outpace N acquisition under warmer conditions in nutrient-limited alpine ecosystems. Although nitrogen-fixing plant species do occur at Finse and locally affect soil nutrient status (Olsen et al. 2013), they are relatively rare and likely do not occur in high enough densities to significantly increase tissue N in neighboring plants (Olsen 2011). We did not find studies at Finse that measured N fixation in response to environmental manipulation or ambient climate change, neither for plants, lichens, or free-living microorganisms.

Short-term experimental warming increased the reproductive output (i.e., number of seeds and seed weight) of the annual facultative hemiparasite *Euphrasia frigida*, while its population density was only affected to a minor extent (Nylén and Totland 1999). Similarly, seed set of the perennial snow bed forb *Saxifraga stellaris* (syn. *Micranthes stellaris*) increased and phenology accelerated under (short-term) experimental warming (Sandvik and Totland 2000), and increased seed weight and advanced flowering was also found for the late-flowering *Leontodon autumnalis* L. in response to 2 years of experimental warming (Totland 1997a). On the other hand, long-term warming did not affect fruit production in *Silene acaulis* (L.) Jacq. and cushion vigor decreased after 18 years of warming by OTCs (Rozite-Arina 2020). Further, fruit production of *S. acaulis* (Rozite-Arina 2020) and seed production and seed mass of *S. stellaris* were positively correlated with plant size (Sandvik et al. 1999). Snow bed specialists such as *Ranunculus glacialis* L. need to flower and produce seeds fast to complete their entire life cycle within the short growing season. However, *R. glacialis* showed no growth, reproductive, or phenological responses to experimental warming (Totland and Alatalo 2002). In contrast to other *Ranunculus* species at Finse, *R. glacialis* flowers maintain their petals after fertilization, which protects the developing seeds from adverse weather conditions (Ida and Totland 2014).

Communities and species interactions

Experimental warming alone had no effect on the diversity of plant communities in the *Dryas* heath at Sanddalsnuten after 4 years (Klanderud and Totland 2005b). Moreover, even after 16 years of warming, community compositions of lichens and vascular plants did not differ between experimentally warmed and control plots (Hasvik 2018), but some small changes in community composition after seven years of experimental warming were found in another experiment in the *Dryas* heath by Olsen and Klanderud (2014b). In addition, total species cover and richness did not respond to 16 years of experimental warming, although lichen richness was lower and forb richness higher in experimentally warmed compared to control plots (Hasvik 2018). Bryophytes responded more strongly to experimental warming than vascular plants and lichens (Van Zuijlen et al. 2022a, 2022b). Specifically, bryophyte species abundance increased over time under ambient warming but not in experimentally warmed plots. Further, experimentally warmed plots featured a larger change in species composition driven by de-

clines in the abundance of *Dicranum* spp. and *Racomitrium* spp. while *Brachythecium albicans* (Hedw.) Schimp. was favored (Van Zuijlen et al. 2022a).

Community stability may be related to diversity, and Klanderud and Totland (2008) showed that initial high species richness, which is characteristic for the alpine *Dryas* heaths, was associated with a stable vascular plant species composition under experimental warming. However, the stability of the vascular plant community composition decreased with nutrient addition. Moreover, the addition of nutrients had significant effects on community composition and more so in plots with high initial species richness (Klanderud and Totland 2008). As such, nutrient addition reduced plant species diversity due to a shift towards graminoid dominance at the expense of dwarf shrubs, lichens, and bryophytes in combination with a >50% increase in community biomass (Klanderud and Totland 2005b). The dominance of graminoids was maintained 6 years after nutrient addition was ceased, indicating that dominance shifts are not readily reversed. Grazing by herbivores, however, increased the rate of recovery towards the original species composition (Olsen and Klanderud 2014b).

The responses of soil arthropod communities to experimental environmental change at Finse mirror the responses of vascular plants in many regards. For instance, few Collembola species responded to warming alone, whereas nutrient addition caused strong changes in the dominance hierarchy of Collembola, an increase in the abundance of predatory mites, and a decrease of Oribatida diversity (Hågvar and Klanderud 2009). Nutrient addition had little effect on other taxa such as Diptera (larvae), but *Arctorthezia cataphracta* (Olafsen, 1772) (Coccoidea) decreased in abundance in concert with decreases in its host plant (*D. octopetala*) abundance, indicating that nutrient addition affects the system across trophic levels (Hågvar and Klanderud 2009). Nine years after cessation of the treatments, Roos et al. (2020) found persistent legacy effects of nutrient additions on Collembola and Oribatida community composition, while their abundance had recovered to control levels. In contrast to vegetation (Olsen and Klanderud 2014b), the presence of herbivores did not consistently affect recovery rates of soil arthropod communities (Roos et al. 2020).

A series of removal experiments showed how species interactions may change in response to environmental change at Finse. These studies concluded that individual plant performance (Klanderud 2005; Klanderud and Totland 2005a), recruitment (Klanderud 2010), plant community structure (Totland and Esaete 2002), and their response to environmental change is affected by a balance between facilitation and competition. Facilitation by neighbors increased plant performance in terms of leaf length and height of some species at Finse (Klanderud 2005; Klanderud and Totland 2005a; Kjær et al. 2018). However, competition was more important for recruitment and species richness at the community level, in particular in the heaths dominated by *D. octopetala* (Klanderud and Totland 2004; Olsen and Klanderud 2014a). Moreover, combined removal and warming experiments suggested that the strength of competitive interactions will increase in warmer climates and may be further enhanced by

nitrogen deposition (Klanderud and Totland 2005b), likely resulting in decreased species diversity.

Herbivory by insects increased under experimental warming, but the dynamics underlying interactions between plants and insects are complex and likely depend on species-specific food preferences and phenology (Birkemoe et al. 2016). The higher herbivory on alpine plants with experimental warming shows that plant survival and composition may be affected by environmental change, but parasitoids may regulate a potential increase of herbivores. The parasitoid diversity has not been fully investigated at Finse, but a limited 1 year-sampling with sticky traps in the *Dryas* heath identified 33 species by using DNA barcoding (Kankaanpää et al. 2020).

Flowering plants at Finse are visited by many different potential pollinator species. Diptera is the most common (Totland 1993; Totland 1994a; Östman 2018), but bumblebees (e.g., *Bombus alpinus* (Linnaeus, 1758)) and butterflies (e.g., *Boloria napaea* (Hoffmansegg, 1804)) also visit flowers of, e.g., *Silene acaulis* (Hovde 2021; R.E. Roos 2020, personal observations). The success of plant sexual reproduction is determined by both environmental conditions and biotic interactions, as is illustrated by several studies on *Ranunculus acris* at Finse (e.g., Vassvik 2019). As such, variation in reproductive success of *R. acris* varied across environmental factors such as soil pH (Totland and Birks 1996), but *R. acris* is self-incompatible and therefore depends on successful pollination by insects (Totland 1997b). Moreover, these biotic and abiotic factors likely interact, as *R. acris* seed production increased when plants were subjected to both increased pollen availability and more favorable wind and temperature conditions under experimental warming treatments (Totland and Eide 1999). Further, seed set and insect visitation rates were higher for *R. acris* individuals that flowered early in the season (Totland 1994b), and the reproductive success of the late-flowering *Leontodon autumnalis* decreased as the flowering season progressed, possibly due to climatic severity and increased extent of pollen and resource limitation (Totland 1997a). Across a snowmelt gradient, *R. acris* showed strong synchrony between flowering phenology and pollinator activity, constant pollinator visitation rate, and no evidence for pollen limitation across the whole growing season (Östman 2018). Heterogeneity in the landscape (i.e., snow melt out dates) may thus buffer against any phenological mismatches as pollinator activity tracks patches of highest flower abundance at any particular time in the season for a generalist species (habitat and pollinators) such as *R. acris* (Östman 2018).

Community-level traits and ecosystem processes

After 16 years of experimental warming, community-level traits of vascular plants shifted towards resource conservative values, in contrast to the expected shift towards more resource acquisitive trait values (Van Zuijlen et al. 2022b). Furthermore, non-vascular primary producer groups showed contrasting trait responses: while bryophytes' specific shoot length increased and carbon concentration and water-holding capacity tended to decrease, as expected under increased competition by vascular plants, no such response was found for lichens (Van Zuijlen et al. 2022b).

Similar paradoxical community-level trait responses were found by Roos et al. (2019) across an elevational gradient as vascular plant and lichen tissue N concentration, specific leaf area, and specific thallus area increased with increasing elevation. The relative importance of intraspecific variation and species turnover as drivers of trait variation in plant communities differed between primary producer groups as well as between traits, both in response to experimental warming (Van Zuijlen et al. 2022b) and across an elevational gradient (Roos et al. 2019). In both cases, bryophytes showed low levels of intraspecific variation, whereas interspecific variation contributed more strongly to variation in chemical or nutritional traits in vascular plants and lichen traits.

Across the same elevational gradient as Roos et al. (2019), community-level concentrations of vascular plant phenolic compounds decreased with elevation while lichen phenolic compounds increased (Asplund et al. 2021). For vascular plants, these changes were mainly driven by shifts in species composition while within-species variation often was negligible. For lichens, changes in sun-screening compounds were driven by both changes in species composition and within-species variation. Interestingly, there were pronounced shifts in the composition of phenolic compounds at the community level. As such, plant phenolic compounds related to biotic stressors (e.g., herbivores and pathogens) were more abundant at low elevations while some antioxidants were more abundant at high elevations, in accordance with predictions (Asplund et al. 2021).

The litter production of vascular plants increased in response to nutrient additions combined with experimental warming (Olsen and Klanderud 2014b) but litter water content and bacterial abundances decreased in warmed plots (Jeanbille et al. 2022). In contrast to the amount of litter, the decomposability of lichen and bryophyte litter (i.e., litter quality) was found to increase with increasing elevation and thus colder temperatures, suggesting that a warmer climate could favor species with lower litter quality and slower decomposition (Van Zuijlen et al. 2020b). In addition, decomposition rates of tea bags were lower in experimentally warmed but higher in warmed and fertilized plots relative to controls (Haakonsen Karr 2017). In a lichen transplant experiment, single-species lichen mats altered soil microclimate and plant litter decomposition, although these effects on microclimate and litter decomposition were unrelated (Van Zuijlen et al. 2020a). Further, species turnover effects were a more important driver of decomposability than intraspecific variation (Van Zuijlen et al. 2020b). There were no effects on soil amino acid nitrogen content (Andresen et al. 2022) or bacterial abundances, but a decrease in soil C:N (Jeanbille et al. 2022) after 14 years of experimental warming in a *Dryas* heath at Finse.

Discussion

In this study, we synthesize three decades of research on ecological responses to environmental change performed at or near the ITEX site at alpine Finse, Norway. Our results show that the climate at Finse is warming at a modest rate. Further, individual species respond to warming in terms of their

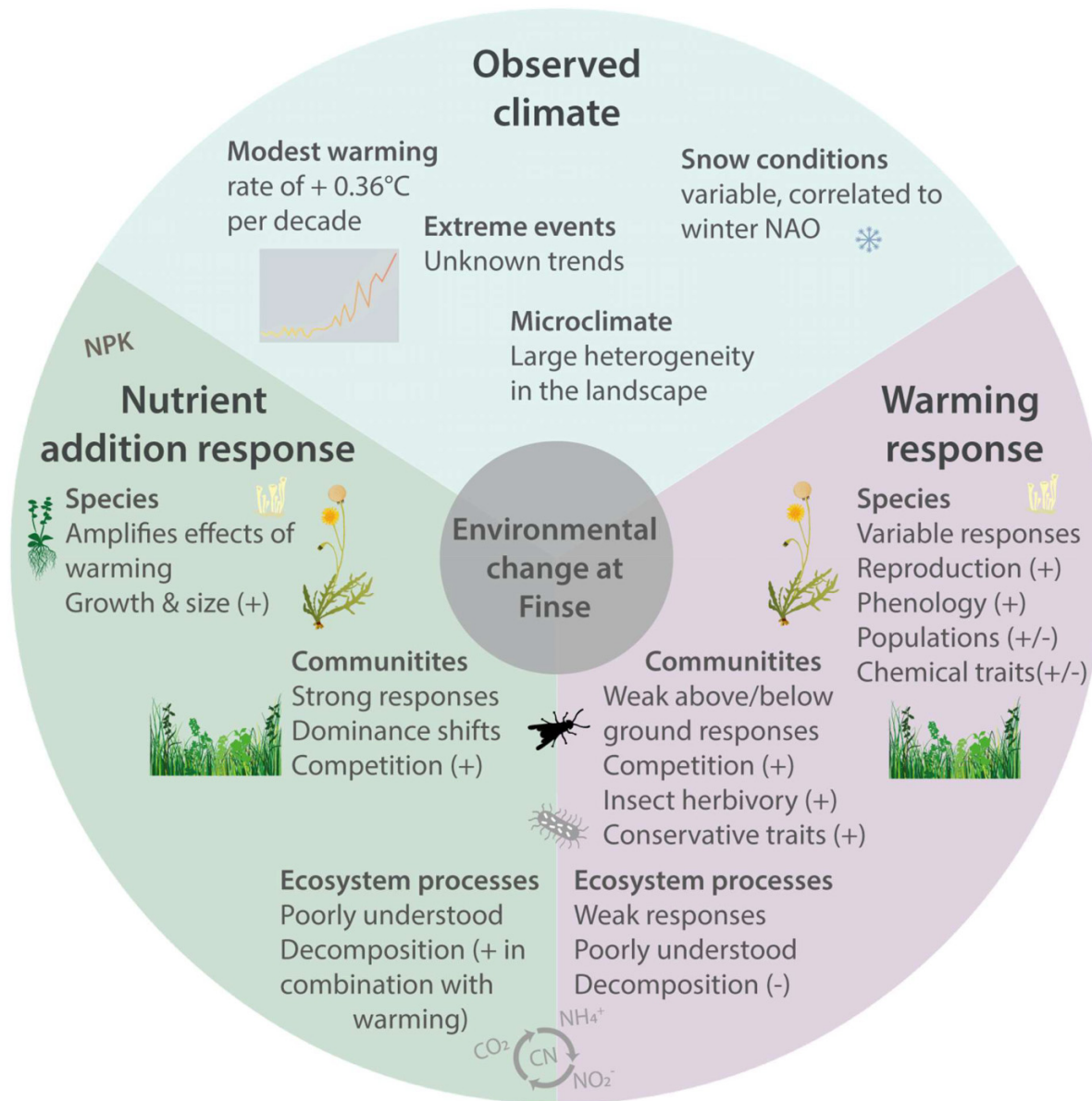
population dynamics, functional traits, and phenology but such species-specific responses do not necessarily translate into changes at the community level (Fig. 6). At Finse, experimental, long-term observational, and gradient approaches have been used to test the effects of environmental change, but not all approaches have been used within each organism group or ecological scale. Here, we discuss how current and future environmental change and the subsequent ecological responses found at Finse compare to other relevant Arctic and alpine sites.

Ecological responses to environmental change

We found an increase of $+0.36$ °C per decade in annual temperature at Finse, which is lower than the Norwegian national average of $+0.5$ °C per decade over the recent (1976–2014) warming period (Hanssen-Bauer et al. 2017). In contrast to the national trend (i.e., strongest increase in spring and autumn, 1900–2014; Hanssen-Bauer et al. 2017), autumn is the season with the strongest warming trend at Finse. We did not find a significant increase of winter temperatures at Finse, which is in correspondence with national trends over 1900–2014. Even though winter temperatures have been measured over a much longer timescale nationally, large interannual variations obscure trends (Hanssen-Bauer et al. 2017). Compared to Finse, the weather station at the most similar alpine ITEX site in Latnjajaure, Sweden, at 950 m a.s.l., reported a similar warming trend of $+0.3$ °C per decade over 1992–2019 (Scharn et al. 2022). In contrast, some Arctic ITEX sites report much stronger warming rates, such as $+1.0$ °C per decade (1990–2003) at Alexandra Fiord, Canada (Hill and Henry 2011) and $+1.66$ °C per decade during 1991–2018 at Svalbard airport close to the ITEX site at Endalen, Svalbard (Jónsdóttir et al. 2022).

The relatively modest increase in temperature over the last decades at Finse did not translate into a significantly prolonged growing season or an increase in accumulated GDD. Moreover, the vascular plant community composition in the *Dryas* heath at Finse showed only minor responses to either ambient (Olsen, personal communications) or experimental warming (Hasvik 2018) after 16 years. However, bryophytes responded negatively to experimental warming at Finse, which is in line with the general trend across ITEX sites (Elmendorf et al. 2012a), but contrasts with the increase in bryophyte cover in OTCs at Alexandra Fiord (Hudson and Henry 2010). The relative resistance of vascular plant communities to temperature increase is not unique to Finse (Hudson and Henry 2010; Körner and Hiltbrunner 2021), and earlier ITEX syntheses revealed that plant communities respond more strongly to warming in moist than dry sites (Elmendorf et al. 2012b). The *Dryas* heath at the Finse ITEX site is located on a well-drained, sun-exposed slope and is therefore dry during most of the growing season, despite relatively high annual precipitation. In addition, moisture regime was found to be an important driver of plant community responses to 26 years of experimental warming in Latnjajaure (Scharn et al. 2022). At the ITEX site in the High-Arctic Svalbard, the community composition of *Dryas* heath did change after 17 years of ambient and experimental warming, but these changes

Fig. 6. Graphical summary of the observed climate and climate trends at Finse and of the ecological responses to experimental and ambient environmental change at Finse over the past three decades. The top segment “observed climate” refers to the observed trends and dynamics of the climate at Finse. The right segment “warming response” summarizes the observed responses individual species, communities, and ecological processes to both experimental and ambient climate change. The left segment “nutrient addition response” summarizes the observed responses of species, communities, and ecological processes to experimental nutrient addition.



were relatively modest and most likely related to an extended growing season (Jónsdóttir et al. 2022, personal communications). It is important to note that a shift in baseline climate may come with an increased frequency of extreme events, such as excessive precipitation, mid-winter warming, rain-on-snow events, temperature anomalies (both positive and negative; see Panchen et al. 2022), and drought. The work so far performed at Finse focuses on persistent changes in average climatic conditions, but extreme events may have disproportionately large and long-lasting effects on species composition and distribution compared to their duration

(Jentsch et al. 2007; Smith 2011; De Boeck et al. 2018). More research is therefore needed on how extreme events drive changes in functioning of the alpine ecosystem (Panchen et al. 2022), and how well experiments capture natural events (Kröel-Dulay et al. 2022) at Finse and elsewhere (Fig. 6).

We currently lack detailed projections of how the climate at Finse may change in the coming decades, but Finse is included in the models specified for West Norway by Hanssen-Bauer et al. (2017). Here, the median projected temperature change for 2071–2100 compared to 1971–2000 is +2.3 °C and +3.9 °C, under scenario RCP4.5 and RCP8.5, re-

spectively. These changes would translate into an elongation of the growing season (defined as the number of days above 5 °C) of 30–60 days in 2071–2100, compared to 1971–2000 (Hanssen-Bauer et al. 2017). However, temperatures recorded at weather stations such as used in this study as well as climate model output are for 2 m above ground and may not necessarily translate well to the temperatures that low-stature alpine plants actually experience during the growing season (Graae et al. 2012; Körner and Hiltbrunner 2018). Therefore, efforts to compare data from the weather station to the microclimate of the Finse ITEX site are underway (Roos et al. 2022), and we encourage ecologists to collect weather data at a level relevant to their study organism.

In West Norway, increases in temperature and growing season length are expected to go in parallel with an increase in precipitation and atmospheric nitrogen deposition of 20%–40% in the period 2071–2100 compared to 1961–1990 (Hole and Engardt 2008). The combined impact of future increased nitrogen deposition and warming may be more severe than that of the warming observed to date, as experimental nutrient addition had strong effects on individual plants (Sandvik and Totland 2000; Klanderud 2008) and bryophytes (Sandvik and Heegaard 2003), as well as plant and micro-arthropod community composition at Finse (Klanderud and Totland 2005b; Hågvar and Klanderud 2009; Olsen and Klanderud 2014b). Similarly, stronger responses to experimental nutrient addition compared to warming have also been found at other ITEX sites (e.g., Van Wijk et al. 2004; Jägerbrand et al. 2009). Generally, alpine and tundra ecosystems are nutrient-limited (Shaver and Chapin 1986) and increases in nutrients due to either deposition or increased nutrient cycling rates in response to warmer conditions, are expected to have a strong impact on alpine vegetation and carbon cycling (Dawes et al. 2017; Li et al. 2021). Our synthesis, however, revealed that there are very few studies on how environmental change may affect soil microbial community compositions at Finse and how this would translate to altered nutrient dynamics.

Our synthesis of research performed at Finse showed that the distribution and population dynamics of many different taxa (e.g., vascular plants, lichens, bryophytes, arthropods, and mammals) depend on heterogeneity in the landscape and, subsequently, local climatic conditions (Fig. 6). As such, snow is an important driver in alpine and tundra ecosystems as it modulates the temperature organisms experience during winter, moisture availability during the growing season, and growing season length (Bokhorst et al. 2016; Happonen et al. 2019; Niittynen et al. 2020; Frei and Henry 2021; Rixen et al. 2022). At other sites, deeper snow during winter strongly affects plant communities or amplified the effects of experimental warming (Wahren et al. 2005; Leffler et al. 2016), while other studies report idiosyncratic responses to snow manipulation (Rumpf et al. 2014). At Finse, changes in snow regimes may be most important to snowbed specialists, which are already well-represented on the list of endangered species in Norway (Artsdatabanken 2021). However, snow dynamics depend on an interplay between landscape topography, winter precipitation and temperature, as well as weather conditions during snow melt in spring. Predicting the length of the future snow season is, therefore,

challenging. In general, snow cover duration in Norway is expected to decrease, but this effect is relatively weak at high elevations due to sufficiently low temperatures during precipitation events (Hanssen-Bauer et al. 2017). In this study, we used snow depth measurements acquired at a single site (i.e., the Finse weather station) and found considerable interannual variation but the relative distribution of snow throughout the landscape is likely comparable between years. We believe that the implementation of remote-sensing methods such as time-lapse imagery (Filhol et al. 2019) and satellites (Niittynen and Luoto 2018) can improve our understanding of how ecological communities and processes depend on snow dynamics across the landscape.

Maximum snow depth recorded at the Finse weather station correlated with the winter NAO regime, and this introduces the possibility to use the NAO as a proxy for snow accumulation across the landscape. As such, NAO is an important driver of climate variability and change across the Atlantic and Europe (Delworth et al. 2016), and clear advances have been made in the seasonal predictability of NAO phase and amplitude (Dunstone et al. 2016; Wang et al. 2017). However, further improvement of our understanding of internal NAO variability and its response to climate change is crucial to future model predictions of winter temperature and precipitation across decadal scales (Athanasiadis et al. 2020; Smith et al. 2020). It is important to note that any effects of NAO are superimposed on those of anthropogenic climate change, potentially alternately masking and enhancing the trends expected under scenarios of climate change (Deser et al. 2017; Iles and Hegerl 2017). At this point, predicting to what extent anthropogenic climate change may lead to a preferential occurrence of either a positive NAO, resulting in dominating westerlies and subsequently more snow accumulation at Finse, or negative NAO phase, or how NAO-phase amplitude is affected, remains an active field of research.

Scaling up from species to communities and ecosystem processes

The responses of plant and animal communities to environmental change can manifest through changes in species population dynamics and distributions, phenology, and morphological and physiological traits (including underlying genetics) (Bellard et al. 2012). Although individual plant species showed changes in population dynamics in response to environmental manipulations at Finse (Fig. 6), we know little about how this affects their distribution at a larger scale. For example, we lack evidence for increasing biodiversity at high elevation such as found in other mountain areas (Steinbauer et al. 2018), and data on whether invasive, low-land species manage to establish in warm or disturbed microsites at Finse such as elsewhere in the alpine (Pauli et al. 2012; Lembrechts et al. 2016, 2018; Rashid et al. 2021). Contrasting species-specific responses to environmental manipulation suggest that there is no one general response to environmental change, which increases the relevance and need of studies at the community level that show the collective outcome of individual species population dynamics and interactions.

Although individual plant species (Klanderud 2008) and plant community functional composition (Van Zuijlen et al. 2022b) responded to experimental warming at Finse, the effect on the *Dryas* heath plant community species composition was limited (Klanderud and Totland 2005b; Hasvik 2018), suggesting that the community is relatively resistant to changes in temperature. This is in line with findings from other ITEX sites (e.g., Hudson and Henry 2010; Lamb et al. 2011; Jónsdóttir et al. 2022, personal communications) and could be related to climatic context, i.e., that responses are less pronounced at sites with drier conditions (Elmendorf et al. 2012b; Scharn et al. 2022). In addition, the *Dryas* heath at the Finse ITEX site is relatively species rich (on average approximately 45 vascular and non-vascular plant species per 0.25 m² plot; Hasvik 2018), and biodiversity may buffer the effects of environmental change at Finse (Klanderud and Totland 2008) and other ecosystems (Hautier et al. 2015), although contrasting results are described and discussed by Hudson and Henry (2010). However, the stability of complex ecosystems containing many species and their interactions should be quantified and interpreted at different scales, depending on the measure (e.g., species, traits, communities) and perturbation (e.g., periodic events, persistent changes, or both combined) applied (Kéfi et al. 2019).

Functional traits are a tool to translate taxonomic responses to environmental change into ecological functioning (e.g., Violle et al. 2007). Theoretically, ameliorated environmental conditions should shift plant traits towards those associated with fast returns on investment and acquisitive resource strategies such as increased specific leaf area and increased tissue nutrient status (Wright et al. 2004). However, studies on primary producer community-level traits in response to experimental warming and across elevation showed little or contrasting responses (Roos et al. 2019; Van Zuijlen et al. 2022b), similar to some other alpine sites (Sundqvist et al. 2013). At the biome-wide scale, environmental drivers were found to structure not only individual plant traits but also trait combinations and trade-offs, which limits the number of successful trait combinations that can persist as environmental conditions change (Bjorkman et al. 2018). As such, communities dominated by long-lived, stress-tolerant species (e.g., *D. octopetala*) may respond less than communities with larger biological productivity (Hudson and Henry 2010), especially when amelioration of one environmental variable (e.g., temperature) coincides with an increase in other environmental stressors (e.g., summer drought, reduced snow cover). We therefore suggest that the modest community-level trait responses at Finse may be due to the harsh environment at Finse, ensuring stable community compositions, limited establishment of new species, and maintaining the conservative trait strategies of existing plant communities.

Plant traits may have afterlife effects (e.g., through litter) that impact ecological processes such as decomposition and ultimately carbon and nutrient cycling (e.g., Cornelissen et al. 2004; Makkonen et al. 2012). In a warmer climate, decomposition rates and nutrient turnover may be expected to increase (see Davidson and Janssens 2006), but a recent review on decomposition in the alpine showed strong contrasts in

responses to environmental factors, although soil moisture generally had a positive effect on decomposition rates (Rawat et al. 2021). Because the experimental warming at Finse and other sites may lower soil moisture (Dabros et al. 2010), any decreases in decomposition rates may in fact not be due to increased temperature but due to low soil and litter moisture. Decomposition and nutrient cycling are complex processes that depend on multiple drivers (litter quality, decomposer communities, and environmental conditions) that act at different scales (Bradford et al. 2017). More research is thus required to fully understand how environmental change may affect decomposition and subsequent processes such as nitrogen cycling and net ecosystem respiration.

Even in cases where environmental change does not affect species diversity, traits, or community composition, the interaction between species could be altered in time (i.e., phenology) and space. For example, there is evidence from Arctic and alpine sites that warming causes a contraction of the flowering season at the community level (Høye et al. 2013; Prevéy et al. 2019) resulting from changes in species' phenology and could lead to potential mismatches between plants and pollinators (Wheeler et al. 2015). However, at Finse, heterogeneity in microclimatic conditions may create phenological gradients, increasing the stability of biotic interactions. Detecting such mismatches requires long-term, systematic collection of phenological and climate data that is not available from Finse. However, the studies included in this within-site synthesis allow us to compare the responses to environmental change at different scales within the ecosystem at Finse: from changes in species to communities, from taxonomic to functional responses, and effects across trophic levels.

Conclusions and future outlook

In this review, we used three decades of ecological research to synthesize the responses of the alpine ecosystem at Finse to environmental change. Although the 80 studies included in this synthesis were not initiated under the umbrella of one comprehensive research project, together they integrate responses from species to the community level, describe species interactions within and across trophic levels, and cover both taxonomic and trait-based approaches. In addition, they reveal several research gaps that we suggest exploring in future research.

Based on the data included in this synthesis, we conclude that climate at Finse is warming at a moderate rate, with minor effects on growing season length and temperatures to date. Landscape heterogeneity and associated variation in microclimate, including snow dynamics, play an important role in the distribution of species at Finse, and heterogeneity may buffer against the effects of environmental change (Post et al. 2009; Suggitt et al. 2018). Experimental warming has had only marginal effects on the alpine plant communities at Finse. However, soil moisture and ambient warming are known drivers of diversity and functional responses of alpine communities (Elmendorf et al. 2012a; Bjorkman et al. 2018), and the cool temperatures in combination with relatively dry conditions that persist in the *Dryas* heath at Finse may

help explain our findings. Nevertheless, warming may still have important effects on individual alpine species' life history, reproductive output, and phenology and thereby interactions with other species. In contrast to warming, nutrient addition strongly impacts plant and soil arthropod communities at Finse, and its effects are further amplified in combination with warming. Collective work from Finse shows that species interactions involving competition, facilitation, herbivory, and predation are important modulators of responses to environmental change, although this literature is biased towards vascular plants.

Considering future predictions of environmental conditions at Finse, our work identifies several lines of further research that will strengthen our understanding of ecosystem structure and functioning. First, precipitation is an axis of environmental change (e.g., Vandvik et al. 2020) left unexplored at Finse so far. As such, the effects of altered precipitation regimes in terms of rain and snow could be combined with existing manipulations of temperature and nutrient status to uncover possible synergistic effects on alpine communities. Further, the work summarized here assumes constant changes in environmental conditions, neglecting the potentially large ecological effects that may accompany episodic or extreme climatic events such as drought. Although the significance of nutrient manipulations at Finse is on par with conclusions from other alpine sites (Bowman et al. 2015; Bowman et al. 2018), it is unknown to what extent the addition of fertilizer accurately simulates natural pathways of altered nutrient availability. Moreover, we lack understanding of interactions between above- and belowground (i.e., plant roots, soil fungi, microbes, Metazoa) components of the ecosystem, and how different functional components sensu Strimbeck et al. (2019) affect ecosystem carbon and nutrient fluxes. Finally, the formulation and quantification of threshold levels at which environmental changes irreversibly affect the alpine ecosystem will benefit management goals for biodiversity hotspots such as the *Dryas* heath at Finse.

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Data availability statement

All data analysed in this manuscript is publically available through the Norwegian Meteorological Institute at seklima.met.no.

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Formal analysis: RR

Investigation: RR

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Competing interests

The authors declare there are no competing interests.

Supplementary material

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