

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

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19

20 Abstract

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

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43 **Key words:** alpine ecosystems, climate change, experimental manipulation, ITEX, open top chamber
44 (OTC), within-site synthesis

45 Introduction

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

54 The International Tundra Experiment (ITEX; see Henry and Molau, 1997) was initiated in 1990 to study the
55 potential responses of Arctic and alpine plant species to predicted environmental changes in the tundra
56 biome (e.g. Chapin et al., 1991). The network's success is highlighted by a series of synthesis papers
57 documenting such effects, first in a special issue of *Global Change Biology* where several papers reported
58 species' responses to short-term environmental manipulation across ITEX-sites, introduced by Henry and
59 Molau (1997). For example, Welker et al. (1997) showed that shoot length, photosynthesis and biomass
60 of the abundant circumpolar species *Dryas octopetala* increased under experimental warming across
61 sites. Subsequently, Arft et al. (1999) demonstrated advanced phenology, a short-term response in
62 vegetative growth and an increase in reproductive effort in response to warming across 13 ITEX-sites.
63 However, these responses differed between functional groups and between high-, low-Arctic and alpine
64 sites. Several successive studies showed that shrubs increase the most in abundance with warming, and
65 that vegetation height increases under both experimental (Walker et al. 2006, Elmendorf 2012a) and long-
66 term ambient warming (Elmendorf et al. 2012b) negatively affecting the abundance of bryophytes and
67 lichens. While increased height of the plant community was a clear and consistent trait response to
68 warming across 117 tundra sites, responses of other functional traits lagged behind (Bjorkman et al.,
69 2018). By combining data from experimental warming and long-term monitoring efforts, Prevéy et al.
70 (2019) found that the flowering season contracts as late flowering plants show stronger phenological
71 responses than early flowering species. Although these studies differ in their approaches e.g., utilizing
72 plot-scale observations (Elmendorf et al., 2012b), responses to *in situ* manipulations (Elmendorf et al.,
73 2012a), or compare monitoring, manipulation and space-for-time approaches simultaneously (Elmendorf
74 et al., 2015, Prevéy et al., 2019), they have in common that they synthesize the responses to
75 environmental change within trophic levels, *across* sites.

76 At many study sites, including ITEX-sites, field experiments have been maintained for several decades,
77 and a large amount of data on various components of the local ecosystem has accumulated. As such,
78 researchers and their students concentrate their ecological research at specific sites and subsequently
79 build long-term data series. Therefore, we argue that the time is ripe for *within*-site syntheses of available
80 data, which will increase our understanding of ecosystem responses to environmental change across
81 ecological scales. Such endeavors are relatively novel, but one synthesis of 18 years of ecological
82 monitoring on Herschel Island (Qikiqtaruk), Canada, revealed an increase in growing season length,
83 advanced phenology, taller vegetation, and changes in plant community composition (Myers-Smith et al.,
84 2019). Depending on the data available, within-site reviews can help to disentangle species versus
85 community-level responses to environmental change, and responses to ambient versus experimental
86 environmental changes. Further, they can help clarify interactions across trophic-levels, and allow for
87 comparisons between taxonomy- and trait-based approaches. Finally, they can put the studies at the
88 individual sites into context with the broader, biome-wide syntheses.

89 In this study, we synthesize nearly three decades of observational and experimental ecological research
90 performed at or near the alpine ITEX site at Finse, southern Norway. The main site is located at Mt.
91 Sanddalsnuten (approx. 1500 m a.s.l.), but we include work from several subsites located near Finse
92 between approximately 1200 and 1500 m a.s.l. We first assess how the climate at Finse has changed over
93 the past three decades in terms of temperature, growing season length, the frequency of frost during the
94 growing season, and how local snow conditions have changed. Further, we summarize existing knowledge
95 on species distributions across gradients in elevation, microtopography, and microclimate. Subsequently,
96 we synthesize how alpine species respond to environmental change in terms of their abundance,
97 functional traits, life-history, and phenology. We then describe how the responses of individual species
98 could translate into altered community composition, diversity, and species interactions. Finally, we
99 discuss how altered species interactions and traits at the community-level may translate into altered
100 ecosystem processes. This synthesis illustrates the important insights that can be acquired from the
101 collective research performed at one site and serves as a basis to further substantiate our understanding
102 of climate change effects on the alpine ecosystem.

103

104 Methodology

105 *Site description*

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

115 *Climate data and analyses*

116 *Climate and weather data from Finse*

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

133 microclimate to average out on a monthly time scale. Snow depth data were collected daily from 1969 to
134 1994 at the Finse station at 8 am by an observer. Unfortunately, no data on snow depth were available
135 for the Finsevatn weather station between its establishment in May 2002 and 2017. Because the data
136 series at Finsevatn would consist only of four years (i.e., 2017-2020) and the two weather stations are at
137 locations with different snow dynamics, only snow depth data from the Finse station were analyzed.
138 Information about the weather stations and the data they record can be found at the station overview of
139 the Norwegian Meteorological office at SeKlima.no (2020b).

140 *[Annual and seasonal temperature trends](#)*

141 To calculate decadal trends in annual and seasonal temperatures, we used monthly average 2 m
142 temperature data from both weather stations. All missing monthly values (Supplementary Table S1) were
143 substituted with interpolated monthly average temperatures provided by the Norwegian Meteorological
144 office (MetNorge, 2020). The substituted data consisted of interpolated daily mean temperatures for the
145 1 × 1 km grid cell closest to Finse, based on values recorded at nearby weather stations and interpolated
146 using a Bayesian Optimal Interpolation method that incorporates the effects of elevation (Lussana et al.,
147 2018). From these interpolated daily average temperatures, monthly means were calculated. Interpolated
148 monthly temperatures correlated strongly with those observed at both weather stations (R^2 of 0.997 for
149 Finse and 0.995 for Finsevatn, respectively, see Supplementary Figure S1). Winter was defined as
150 December through February, spring as March through May, summer as June through August, and autumn
151 as September through November. To test for decadal trends, we performed simple linear regression
152 analyses in R version 4.0.0 (R Core Team, 2020).

153 *[Growing seasons, growing degree days, and frost days](#)*

154 We calculated the approximate growing season start, end, and length based on daily 2 m average
155 temperatures from the two weather stations at Finse. In the alpine, the growing season starts as soon as
156 the snow melts. To calculate the length and accumulated warmth of the snow free growing season, we
157 use two different temperature thresholds: a daily average of 5 and 0 °C. As such, 5 °C is a common
158 threshold used to define plant growth (Maxwell, 1992), but is likely a conservative estimate for the
159 growing season in the Arctic and alpine. On the other hand, the 0 °C threshold may be an optimistic
160 estimate, as snow can persist while daily average temperatures have risen above freezing. Specifically,
161 the start of a season was defined as the first day of the first block of at least five days above the threshold
162 temperature, and the end as the last day in the last block of at least five days above the threshold, for

163 each year. To exclude warm periods in mid-winter, the 5 °C growing season was calculated between day
 164 of year (DOY) 91 and 304, and the 0 °C growing season between DOY 60 and 334. Years missing more than
 165 10 days of average temperature data during these periods were excluded from further analyses (year
 166 1969, 1982, 1991, 1994 through 2004, and 2012). For any remaining days with missing average
 167 temperature data (i.e. for years with less than 10 days with missing data), the daily average temperature
 168 was calculated as the average (T_{avg}) of the daily minimum and maximum temperatures on that day (for
 169 43 days in the dataset). Subsequently, we calculated accumulated thawing degree days (TDD) using the 0
 170 °C threshold (T_{base}) and accumulated growing degree days (GDD) using the 5 °C threshold. Thawing
 171 degree days were thus calculated as:

$$172 \sum_{i=60}^{334} GDU_{T_{base}=0^{\circ}\text{C}, i},$$

173 and GDD as:

$$174 \sum_{i=91}^{304} GDU_{T_{base}=5^{\circ}\text{C}, i},$$

175 where *Growing Degree Unit (GDU)* = $\max(T_{avg} - T_{base}, 0)$. Finally, we calculated the number of
 176 frost days (minimum daily temperature below 0 °C) during the 5 °C growing season and 0 °C growing
 177 season for each year. In this analysis, seasons missing more than 10 days of minimum temperatures were
 178 excluded from analysis. To test for temporal trends, we performed simple linear regression analyses in R
 179 version 4.0.0. Separate analyses were performed for each of the weather stations as no interpolated data
 180 were used for daily values to fill the 1994 - 2002 data gap.

181 *Snow and its relation to NAO*

182 The reported average yearly precipitation for Finse is 1030 mm over 1969-1990 (Førland, 1993), and we
 183 found no significant trend over time in total annual precipitation over 1969 – 2020 (Estimate = -18 mm
 184 decade⁻¹, $R^2 = 0.02$, $p = 0.423$, Supplementary Figure S2). In winter, precipitation falls as snow, and the
 185 landscape is typically snow-covered from November to May, but in some years snow can persist through
 186 summer across substantial parts of the landscape (Roos 2020, *personal observations*). In our analyses, we
 187 use snow depth data from the Finse weather station (i.e. winter 1970-1994). We then used a simple linear
 188 model in R version 4.0.0 to test for trends in maximum snow cover over time. Further, to explore how
 189 local snow conditions relate to, and can possibly be predicted by, large-scale atmospheric circulation
 190 patterns, we extracted winter (December-March) North Atlantic Oscillation (NAO) indices (principal

191 component-based) *sensu* Hurrell and Deser (2010) from the Climate Data Guide database (NCAR, 2020)
192 and correlated these to the maximum daily observed snow depth (December-March) at the Finse weather
193 station (1970-1994). A positive NAO-phase indicates a zonal flow pattern with low pressure around
194 Iceland in combination with a strong Azores High and thus the dominating Westerlies over NW-Europe.
195 In contrast, a negative NAO-phase corresponds to more meridional flow over the North Atlantic and thus
196 reduced westerly flows and greater frequencies of dry and easterly weather patterns in NW-Europe
197 (Hurrell, 1995). To test for any differences in maximum snow depth between winters with an overall
198 positive versus those dominated by a negative NAO-pattern, we used a Wilcoxon rank sum test with
199 continuity correction in R version 4.0.0. To test whether deep snow cover translates to late snow melt
200 out, we correlate maximum winter snow depth with snow melt-out date (first day of the year without
201 snow depth recorded). Years with missing data (1976 through 1980, 1992, and 1994), and those with an
202 unrealistic drop in snow depth i.e., a snow-free day succeeding a day with >50 cm snow depth (1970 and
203 1972), were excluded from analyses.

204 *Literature synthesis*

205 Our synthesis on ecological responses to environmental change at Finse is based on previously published
206 literature. To find relevant literature, we performed a search in ISI Web of Science using the search criteria
207 “Title: (Sanddalsnuten OR Finse) OR Topic: (Sanddalsnuten OR Finse)”, which revealed 56 hits (September
208 2020). Because ISI Web of Science and other literature databases known to us do not allow searches within
209 the methodology sections of articles or searches on geographical locations, we performed searches in
210 additional databases such as Google Scholar (“Finse” and “Sanddalsnuten”) and the library at the Finse
211 Alpine Research Center. Because several studies known to us were not included in the results of the
212 database searches, we further extended our selection by screening reference lists in selected literature,
213 and knowledge of studies and authors through our own work. Studies were eligible for inclusion in this
214 review if their focus was on terrestrial ecology at or near the ITEX-site at Sanddalsnuten or Finse and were
215 relevant to understand ecological responses to environmental change. As such, studies primarily focused
216 on aquatic systems (e.g. rivers and lakes) were not included. Moreover, studies in geology, glaciology and
217 physics were only included if they were ecologically relevant. To plot the study locations on the map
218 (Figure 1), we used ArcGIS Pro v2.5.0 (Esri, 2020).

219 Results

220 *Environmental change at Finse*

221 *Annual and seasonal temperature trends*

222 The average annual temperature at Finse measured over 1970-1990 was -2.0 °C and increased by 0.36 °C
223 per decade over the period 1970-2020 ($R^2 = 0.322$, $p < 0.001$) based on data from both the Finse and
224 Finsevatn weather station, as well as interpolated data. Spring (average -4.0 °C) and summer (+6.4 °C)
225 showed trends of +0.29 °C ($R^2 = 0.144$, $p = 0.006$) and +0.34 °C per decade ($R^2 = 0.192$, $p = 0.001$),
226 respectively. Autumn (average -1.2 °C) showed a more pronounced trend of +0.45 °C per decade ($R^2 =$
227 0.247 , $p < 0.001$). For winter (average -9.1 °C), the decadal trend (+0.38 °C per decade) was not significant
228 (Figure 2).

229 *Growing seasons, growing degree days, and frost days*

230 The average length of the 0 °C growing season was 162 days for Finse (1970 – 1993) and 175 days for
231 Finsevatn (2005 – 2020), while the 5 °C growing season was 83 and 97 days, respectively. The start of the
232 0 °C growing season advanced with 0.89 days per year ($R^2 = 0.327$, $p = 0.007$) over the period 1970 – 1993,
233 and the length of this season therefore also increased with 1.0 day per year ($R^2 = 0.199$, $p = 0.043$, Figure
234 3a, b). Other growing season parameters showed non-significant trends only (Supplementary Table S2).
235 The average thawing degree days (TDD) at Finse (1970 – 1993) was 763 and the average accumulated
236 growing degree days (GDD) was 196, while for Finsevatn (2005 – 2020) 977 TDD and 316 GDD were
237 accumulated annually. At Finse (1970 – 1993) there was a non-significant negative trend in accumulated
238 TDD and GDD, while for Finsevatn (2005 – 2020) TDD showed a non-significant increase over time (Figure
239 3c, Supplementary Table S2). The occurrence of frost during the growing season showed a positive but
240 non-significant trend over time for both time periods, most notably during the 0 °C growing season (Figure
241 3d, Supplementary Table S2).

242 *Snow dynamics*

243 Maximum winter snow depth (1970-1994) varied between 120 cm (1977) and 425 cm (1976), without a
244 significant linear trend through time (estimate = 3.825, $R^2 = 0.07$, $p = 0.222$). For the 16 years where snow
245 depth data were available until snow had completely melted, maximum snow depth was positively
246 correlated with snow melt-out date (slope = +0.14 d cm⁻¹, $R^2 = 0.48$, $p = 0.004$). The maximum winter snow

247 depth observed at the Finse weather station was 2.28 times greater (365 cm versus 160 cm, respectively)
248 in years with a positive NAO (dominating westerlies) compared to years with a negative NAO ($W = 0$, p -
249 value < 0.001 , Figure 4b). In addition, positive NAO winters tended to be milder (Figure 4a), although cold
250 winters with high maximum snow depth have also occurred.

251 *Ecological responses to environmental change at Finse*

252 Our literature search resulted in a total of 80 studies on ecological responses to environmental change at
253 Finse between 1975 and 2022 (Supplementary Table S3 and Figure 5). Most studies focused on plants
254 (both vascular and non-vascular) and lichens (35) and how they interact with insects (9 studies), each
255 other (7 studies), or fungi (three studies) while only six studies focused specifically on ecosystem processes
256 such as decomposition and nutrient cycling (Figure 5). These studies include a variety of experimental
257 approaches, such as environmental manipulations (warming by open top chambers (OTCs) and/or
258 nutrient additions, 28 studies), environmental and successional gradients (21 and 7 studies, respectively),
259 and manipulation of community composition (4 studies) or individuals (2 studies). In the following
260 sections, we first present how microclimate and topography affect the distribution of primary producers
261 (including vascular plants, lichens, bryophytes), arthropods, and vertebrates. Then, we address the results
262 from studies on how environmental change affects the populations, traits, reproduction, and phenology
263 of individual species. Finally, we report the effects of environmental change on taxonomic and functional
264 community composition, species interactions and ecosystem processes

265 *Landscape heterogeneity and microclimatic drivers of species distributions*

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

277 distribution and microclimatic preferences of fungi despite their high abundance and diversity at Finse
278 (Gulden, 1980, Noordeloos and Gulden, 1989) and symbioses with alpine plants (Blaalid et al., 2012, Davey
279 et al., 2015).

280 Microclimatic conditions also drive the distribution of non-sessile organisms at Finse. Although some
281 arthropods, such as oribatid mites that live on rocks, showed remarkable tolerances to drought and
282 extreme cold (Sjursen and Sømme, 2000), different arthropod species occupied separate niches across
283 variation in soil moisture and show contrasting temporal activity patterns (Ottesen, 1996). The
284 distribution of spider species were related to microclimatic condition such as temperature, moisture, and
285 soil nutrient availability (Hauge and Ottesen, 2002). As such, climatically “mild” sites were dominated by
286 lowland spider species, whereas alpine species were common in “severe” (both dry and cold as well as
287 wet and cold) sites. In the low alpine zone where *Salix* shrubs form dense stands, lowland forest spider
288 species were relatively common (Hauge and Ottesen, 2002). Closely related arthropod species whose
289 distribution correlates with the distribution of their host plants (e.g. Psyllidae on *Salix lapponum*) were
290 separated across elevation gradients through thermal requirements and phenological synchronization
291 with the host plant (Hill et al., 1998, Hill and Hodkinson, 1995).

292 The glaciers at Finse, including the large Hardangerjøkulen, are retreating (Giesen and Oerlemans, 2010)
293 and as the ice melts, new parts of the landscape open up for colonization. Paradoxically, consumers such
294 as Collembola, Oribatida, and Coleoptera are often the first organisms to colonize glacial forelands as
295 establishment is generally more limiting than dispersion (e.g., Flø and Hågvar, 2013, Hågvar, 2012, Bråten
296 et al., 2012). Previously, it was assumed that these consumers feed on blown-in plant material and prey
297 animals, but at Finse, Hågvar and Ohlson (2013) showed that both aquatic and terrestrial arthropod
298 pioneer communities (e.g., Coleoptera, Araneae) ate locally derived midges that contained ancient carbon
299 released from the glacier. These findings suggest that the pioneer food chain is based on “old” carbon and
300 challenges the idea that glacial forelands are examples of primary succession uninfluenced by resources
301 from previous ecosystems.

302 Finse features populations of mammals such as rodents (e.g., voles and lemming), mountain hare, wild
303 reindeer, and domestic sheep. Although their population dynamics extend across a spatial scale that is
304 beyond the scope of this site-specific synthesis, the ecology of several mammal species impact the
305 vegetation and soil and is thus relevant to species interactions and ecosystem dynamics at the Finse ITEX
306 site. For example, rodents can affect vegetation by grazing and burrowing (e.g., from nearby Dovrefjell,

307 Nystuen et al., 2014), which has been shown on one particular plant species at Finse, the annual *Euphrasia*
308 *frigida*. For this species, population densities were highest at intermediate levels of rodent disturbance
309 (Nylén and Totland, 1999). Voles (*Microtus* spp.) and lemming (*Lemmus lemmus*) show classic peaks in
310 population densities, but do so less frequently at Finse than in other areas in Fennoscandia (Framstad,
311 2020). Although their population cycles are most often portrayed as density-dependent or driven by
312 predator-prey interactions (Stenseth et al., 1998, Steen et al., 1997), lemming populations at Finse and
313 Hardangervidda may be driven by the availability of food, notably bryophytes (Turchin et al., 2000), plant
314 defense chemicals (Seldal et al., 1994), and (changes in) winter weather and snow conditions (Kausrud et
315 al., 2008, Landa, 2020). Other important grazers in the area are mountain hare (*Lepus timidus*), domestic
316 sheep (*Ovis aries*), and wild reindeer (*Rangifer tarandus* ssp. *tarandus*). Mountain hares exploit a wide
317 variety of plants as food, but preferred forbs (Johannessen and Samset, 1994). While reindeer and
318 domestic sheep overlap considerably in dietary preferences (in summer), their spatial distributions rarely
319 overlap (Skogland, 1984), and sheep are brought to farms at lower elevation in winter. In fact, reindeer
320 avoid the Finse area due to high tourist densities and human infrastructure such as the railway (Gundersen
321 et al., 2019). It is therefore likely that their impact on the vegetation at the ITEX site is minor compared to
322 that of domestic sheep, which visit frequently. Large mammalian predators have been absent from the
323 Finse area in recent times, but arctic fox (Landa et al., 2017) and the invasive American mink do occur
324 (Hagelin, 2016). The complete faunal structure of Hardangervidda, including Finse, was summarized in
325 detail by Solhøy et al. (1975).

326 *Species-specific responses to environmental change*

327 The changes in population density of alpine plant species in response to experimental warming (by OTCs)
328 and nutrient addition were strongly species-specific, both after four years within *Dryas* heath (Klanderud,
329 2008) and after five years in snowbed communities (Sandvik et al., 2004). For example, in the *Dryas* heath,
330 grasses (*Festuca* sp., *Poa alpina*) and *Cerastium alpinum* increased in abundance in response to
331 experimental warming and nutrient addition, while *Tofieldia pusilla* decreased. In the snowbed
332 communities, *Salix herbacea* increased in abundance in response to warming while *Carex lachenalii* and
333 *P. alpina*, among others, did not respond. In many cases, species' responses to warming were amplified
334 by the addition of nutrients (Klanderud, 2008). Although the responses of bryophyte and lichen species
335 were more similar in direction (i.e. a decrease of their abundance, particularly when warming and nutrient
336 addition were combined), the magnitude of the responses varied across individual species (Klanderud,
337 2008). In snow bed habitats, species abundances were already changing under ambient conditions (i.e.

338 the abundances of many of the monitored species were increasing in control plots over the five year
339 duration of the experiment) and these changes were amplified by experimental warming for only some
340 herbaceous species (Sandvik et al., 2004). However, due to a general increase in ramet density and the
341 mean abundance per species, which the authors attribute to a potential increase in nutrient availability,
342 a warmer environment may increase the density of snow bed vegetation (Sandvik et al., 2004).

343 In addition to responses in species' abundance, warming experiments at Finse also affected species'
344 functional traits. For example, experimental warming increased the height of both ridge and leeward
345 vegetation (Nybakken et al., 2011), but the strongest effects on plant size and growth were found when
346 warming was combined with nutrient additions. As such, leaf dry mass of *Dryas octopetala* increased after
347 five years of warming whereas nutrient addition (alone and combined with warming) increased leaf dry
348 weights for *Salix reticulata* and *Bistorta vivipara*, both of which did not respond to warming alone
349 (Nybakken et al., 2008). Further, warming did not increase *Saxifraga stellaris* rosette size (Sandvik and
350 Totland, 2000) or number of leaves of *Thalictrum alpinum* and *Carex vaginata* (Klanderud, 2005), but
351 growth and leaf numbers increased in response to nutrient addition or when warming and nutrient
352 addition were combined (Sandvik and Totland, 2000). Moreover, the growth of the forb *Parnassia*
353 *palustris* did not respond to experimental warming over two years, but warming did positively affect its
354 reproductive traits such as seed number and mass (Sandvik and Eide, 2009). The bryophyte *Pohlia*
355 *wahlenbergii* showed increased growth (shoot length) after four years of warming, and growth further
356 increased when nutrients were also added (Sandvik and Heegaard, 2003). In addition, *P. wahlenbergii*
357 adopted a "laxer" growth form with increased temperature or added nutrients, while no significant
358 interaction was found between the treatments. Because a laxer growth form reduces water holding
359 capacity in bryophytes, such growth responses are only advantageous under continuously moist
360 conditions, such as in snow beds where meltwater is present throughout the entire growing season
361 (Sandvik and Heegaard, 2003).

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

369 *lachenalii* while C concentrations tended to increase. However, this translated into a significant increase
370 in C:N ratio for *C. cerastoides* and *E. anagallidifolium* only (Sandvik and Eide, 2011). This indicates a
371 potential dilution effect where increases in C uptake by photosynthesis outpace N acquisition under
372 warmer conditions in nutrient-limited alpine ecosystems. Although nitrogen-fixing plant species do occur
373 at Finse and locally affect soil nutrient status (Olsen et al., 2013), they are relatively rare and likely do not
374 occur in high enough densities to significantly increase tissue N in neighboring plants (Olsen, 2011). We
375 did not find studies at Finse that measured N-fixation in response to environmental manipulation or
376 ambient climate change, neither for plants, lichens, or free-living microorganisms.

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

391 *Communities and species interactions*

392 Experimental warming alone had no effect on the diversity of plant communities in the *Dryas* heath at
393 Sanddalsnuten after four years (Klanderud and Totland, 2005b). Moreover, even after 16 years of
394 warming, community compositions of lichens and vascular plants did not differ between experimentally
395 warmed and control plots (Hasvik, 2018), but some small changes in community composition after seven
396 years of experimental warming were found in another experiment in the *Dryas* heath by Olsen and
397 Klanderud (2014b). In addition, total species cover and richness did not respond to 16 years of
398 experimental warming, although lichen richness was lower and forb richness higher in experimentally

399 warmed compared to control plots (Hasvik, 2018). Bryophytes responded more strongly to experimental
400 warming than vascular plants and lichens (Van Zuijlen et al., 2022a, Van Zuijlen et al., 2022b). Specifically,
401 bryophyte species abundance increased over time under ambient warming, but not in experimentally
402 warmed plots. Further, experimentally warmed plots featured a larger change in species composition
403 driven by declines in the abundance of *Dicranum* spp. and *Racomitrium* spp. while *Brachythecium albicans*
404 was favored (Van Zuijlen et al., 2022a).

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

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

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

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

446 Flowering plants at Finse are visited by many different potential pollinator species. Diptera are the most
447 common (Totland, 1993, Totland, 1994a, Östman, 2018), but bumblebees (e.g. *Bombus alpinus*) and
448 butterflies (e.g. *Boloria napaea*) also visit flowers of e.g. *Silene acaulis* (Hovde, 2021, Roos 2020, personal
449 observations). The success of plant sexual reproduction is determined by both environmental conditions
450 and biotic interactions, as is illustrated by several studies on *Ranunculus acris* at Finse (e.g., Vassvik, 2019).
451 As such, variation in reproductive success of *R. acris* varied across environmental factors such as soil pH
452 (Totland and Birks, 1996), but *R. acris* is self-incompatible and therefore depends on successful pollination
453 by insects (Totland, 1997b). Moreover, these biotic and abiotic factors likely interact, as *R. acris* seed
454 production increased when plants were subjected to both increased pollen availability and more favorable
455 wind and temperature conditions under experimental warming treatments (Totland and Eide, 1999).
456 Further, seed set and insect visitation rates were higher for *R. acris* individuals that flowered early in the
457 season (Totland, 1994b), and the reproductive success of the late-flowering *Leontodon autumnalis*
458 decreased as the flowering season progressed, possibly due to climatic severity and increased extent of

459 pollen and resource limitation (Totland 1997a). Across a snowmelt gradient, *R. acris* showed strong
460 synchrony between flowering phenology and pollinator activity, constant pollinator visitation rate and no
461 evidence for pollen limitation across the whole growing season (Östman, 2018). Heterogeneity in the
462 landscape (i.e. snow melt out dates) may thus buffer against any phenological mismatches as pollinator
463 activity tracks patches of highest flower abundance at any particular time in the season for a generalist
464 species (habitat and pollinators) such as *R. acris* (Östman, 2018).

465 Community-level traits and ecosystem processes

466 After 16 years of experimental warming, community-level traits of vascular plants shifted towards
467 resource conservative values, in contrast to the expected shift towards more resource acquisitive trait
468 values (Van Zuijlen et al., 2022b). Furthermore, non-vascular primary producer groups showed contrasting
469 trait responses: while bryophytes' specific shoot length increased and carbon concentration and water
470 holding capacity tended to decrease, as expected under increased competition by vascular plants, no such
471 response was found for lichens (Van Zuijlen et al., 2022b). Similar paradoxical community-level trait
472 responses were found by Roos et al. (2019) across an elevational gradient as vascular plant and lichen
473 tissue N concentration, specific leaf area and specific thallus area increased with increasing elevation. The
474 relative importance of intraspecific variation and species turnover as drivers of trait variation in plant
475 communities differed between primary producer groups as well as between traits, both in response to
476 experimental warming (Van Zuijlen et al., 2022b) and across an elevational gradient (Roos et al., 2019). In
477 both cases, bryophytes showed low levels of intraspecific variation, whereas interspecific variation
478 contributed more strongly to variation in chemical or nutritional traits in vascular plants and lichen traits.

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

488 The litter production of vascular plants increased in response to nutrient additions combined with
489 experimental warming (Olsen and Klanderud, 2014b) but litter water content and bacterial abundances
490 decreased in warmed plots (Jeanbille et al., 2022). In contrast to the amount of litter, the decomposability
491 of lichen and bryophyte litter (i.e. litter quality) was found to increase with increasing elevation and thus
492 colder temperatures, suggesting that a warmer climate could favor species with lower litter quality and
493 slower decomposition (Van Zuijlen et al., 2020b). In addition, decomposition rates of tea bags were lower
494 in experimentally warmed but higher in warmed and fertilized plots relative to controls (Haakonsen Karr,
495 2017). In a lichen transplant experiment, single-species lichen mats altered soil microclimate and plant
496 litter decomposition, although these effects on microclimate and litter decomposition were unrelated
497 (Van Zuijlen et al., 2020a). Further, species turnover effects were a more important driver of
498 decomposability than intraspecific variation (Van Zuijlen et al. 2020b). There were no effects on soil amino
499 acid nitrogen content (Andresen et al., 2022) or bacterial abundances, but a decrease in soil C:N (Jeanbille
500 et al., 2022) after 14 years of experimental warming in a *Dryas* heath at Finse.

501

502 Discussion

503 In this study, we synthesize three decades of research on ecological responses to environmental change
504 performed at or near the ITEX site at alpine Finse, Norway. Our results show that the climate at Finse is
505 warming at a modest rate. Further, individual species respond to warming in terms of their population
506 dynamics, functional traits, and phenology but such species-specific responses do not necessarily
507 translate into changes at the community level (Figure 6). At Finse, experimental, long-term observational,
508 and gradient approaches have been used to test the effects of environmental change, but not all
509 approaches have been used within each organism group or ecological scale. Here, we discuss how current
510 and future environmental change and the subsequent ecological responses found at Finse compare to
511 other relevant Arctic and alpine sites.

512 *Ecological responses to environmental change*

513 We found an increase of +0.36 °C per decade in annual temperature at Finse, which is lower than the
514 Norwegian national average of +0.5 °C per decade over the recent (1976-2014) warming period (Hanssen-
515 Bauer et al., 2017). In contrast to the national trend (i.e., strongest increase in spring and autumn, 1900-
516 2014, Hanssen-Bauer et al. 2017), autumn is the season with the strongest warming trend at Finse. We
517 did not find a significant increase of winter temperatures at Finse, which is in correspondence with
518 national trends over 1900-2014. Even though winter temperatures have been measured over a much
519 longer timescale nationally, large interannual variations obscure trends (Hanssen-Bauer et al., 2017).
520 Compared to Finse, the weather station at the most similar alpine ITEX site in Latnjajaure, Sweden, at 950
521 m a.s.l., reported a similar warming trend of +0.3 °C per decade over 1992-2019 (Scharn et al., 2022). In
522 contrast, some Arctic ITEX sites report much stronger warming rates, such as +1.0 °C per decade (1990-
523 2003) at Alexandra Fiord, Canada (Hill and Henry, 2011) and +1.25°C per decade (1989-2011) at Endalen,
524 Svalbard (Jónsdóttir et al. 2022, *personal communications*).

525 The relatively modest increase in temperature over the last decades at Finse did not translate into a
526 significantly prolonged growing season or increase in accumulated growing degree days. Moreover, the
527 vascular plant community composition in the *Dryas* heath at Finse showed only minor responses to either
528 ambient (Olsen, *personal communication*) or experimental warming (Hasvik, 2018) after 16 years.
529 However, bryophytes responded negatively to experimental warming at Finse, which is in line with the
530 general trend across ITEX sites (Elmendorf et al., 2012a), but contrasts with the increase in bryophyte
531 cover in OTCs at Alexandra Fiord (Hudson and Henry, 2010). The relative resistance of vascular plant

532 communities to temperature increase is not unique to Finse (Körner and Hiltbrunner, 2021, Hudson and
533 Henry, 2010), and earlier ITEX syntheses revealed that plant communities respond more strongly to
534 warming in moist than dry sites (Elmendorf et al., 2012b). The *Dryas* heath at the Finse ITEX site is located
535 on a well-drained, sun-exposed slope and is therefore dry during most of the growing season, despite
536 relatively high annual precipitation. In addition, moisture regime was found to be an important driver of
537 plant community responses to 26 years of experimental warming in Latnjajaure (Scharn et al., 2022). At
538 the ITEX site in the high-Arctic Svalbard, the community composition of *Dryas* heath did change after 17
539 years of ambient and experimental warming, but these changes were relatively modest and most likely
540 related to an extended growing season (Jónsdóttir et al., 2022, personal communications). It is important
541 to note that a shift in baseline climate may come with an increased frequency of extreme events, such as
542 excessive precipitation, mid-winter warming, rain-on-snow events, temperature anomalies (both positive
543 and negative, see Panchen et al. (2022)) and drought. The work so far performed at Finse focuses on
544 persistent changes in average climatic conditions, but extreme events may have disproportionately large
545 and long-lasting effects on species composition and distribution compared to their duration (Smith, 2011,
546 Jentsch et al., 2007, De Boeck et al., 2018). More research is therefore needed on how extreme events
547 drive changes in functioning of the alpine ecosystem (Panchen et al., 2022) and how well experiments
548 capture natural events (Kröel-Dulay et al., 2022) at Finse and elsewhere (Figure 6).

549 We currently lack detailed projections of how the climate at Finse may change in the coming decades, but
550 Finse is included in the models specified for West-Norway by Hanssen-Bauer et al. (2017). Here, the
551 median projected temperature change for 2071-2100 compared to 1971-2000 is +2.3°C and +3.9°C, under
552 scenario RCP4.5 and RCP8.5, respectively. These changes would translate into an elongation of the
553 growing season (defined as the number of days above 5 °C) of 30 to 60 days in 2071-2100, compared to
554 1971-2000 (Hanssen-Bauer et al., 2017). However, temperatures recorded at weather stations such as
555 used in this study as well as climate model output are for two meters above ground and may not
556 necessarily translate well to the temperatures that low-stature alpine plants actually experience during
557 the growing season (Körner and Hiltbrunner, 2018, Graae et al., 2012). Therefore, efforts to compare data
558 from the weather station to the microclimate of the Finse ITEX site are underway (Roos et al. 2022,
559 *personal communications*), and we encourage ecologists to collect weather data at a level relevant to their
560 study organism.

561 In West-Norway, increases in temperature and growing season length are expected to go in parallel with
562 an increase in precipitation and atmospheric nitrogen deposition of 20-40% in the period 2071-2100

563 compared to 1961-1990 (Hole and Engardt, 2008). The combined impact of future increased nitrogen
564 deposition and warming may be more severe than that of the warming observed to date, as experimental
565 nutrient addition had strong effects on individual plants (Sandvik and Totland, 2000, Klanderud, 2008) and
566 bryophytes (Sandvik and Heegaard, 2003), as well as plant and micro-arthropod community composition
567 at Finse (Klanderud and Totland, 2005b, Olsen and Klanderud, 2014b, Hågvar and Klanderud, 2009).
568 Similarly, stronger responses to experimental nutrient addition compared to warming have also been
569 found at other ITEX sites (e.g., Van Wijk et al., 2004, Jägerbrand et al., 2009). Generally, alpine and tundra
570 ecosystems are nutrient-limited (Shaver and Chapin, 1986) and increases in nutrients due to either
571 deposition or increased nutrient cycling rates in response to warmer conditions, are expected to have a
572 strong impact on alpine vegetation and carbon cycling (Li et al., 2021, Dawes et al., 2017). Our synthesis
573 however, revealed that there are very few studies on how environmental change may affect soil microbial
574 community compositions at Finse and how this would translate to altered nutrient dynamics.

575 Our synthesis of research performed at Finse showed that the distribution and population dynamics of
576 many different taxa (e.g., vascular plants, lichens, bryophytes, arthropods, and mammals) depend on
577 heterogeneity in the landscape and subsequently, local climatic conditions (Figure 6). As such, snow is an
578 important driver in alpine and tundra ecosystems as it modulates the temperature organisms experience
579 during winter, moisture availability during the growing season, and growing season length (Niittynen et
580 al., 2020, Happonen et al., 2019, Bokhorst et al., 2016, Rixen et al., 2022, Frei and Henry, 2021). At other
581 sites, deeper snow during winter strongly affects plant communities or amplified the effects of
582 experimental warming (Wahren et al., 2005, Leffler et al., 2016), while other studies report idiosyncratic
583 responses to snow manipulation (Rumpf et al., 2014). At Finse, changes in snow regimes may be most
584 important to snowbed specialists, which are already well-represented on the list of endangered species
585 in Norway (Artsdatabanken, 2021). However, snow dynamics depend on an interplay between landscape
586 topography, winter precipitation and temperature, as well as weather conditions during snow melt in
587 spring. Predicting the length of the future snow season is therefore challenging. In general, snow cover
588 duration in Norway is expected to decrease, but this effect is relatively weak at high elevations due to
589 sufficiently low temperatures during precipitation events (Hanssen-Bauer et al. 2017). In this study, we
590 used snow depth measurements acquired at a single site (i.e., the Finse weather station) and found
591 considerable interannual variation but the relative distribution of snow throughout the landscape is likely
592 comparable between years. We believe that the implementation of remote-sensing methods such as
593 time-lapse imagery (Filhol et al., 2019) and satellites (Niittynen and Luoto, 2018) can improve our

594 understanding of how ecological communities and processes depend on snow dynamics across the
595 landscape.

596 Maximum snow depth recorded at the Finse weather station correlated with the winter North Atlantic
597 Oscillation (NAO) regime, and this introduces the possibility to use the NAO as a proxy for snow
598 accumulation across the landscape. As such, NAO is an important driver of climate variability and change
599 across the Atlantic and Europe (Delworth et al., 2016), and clear advances have been made in the seasonal
600 predictability of NAO phase and amplitude (Wang et al., 2017, Dunstone et al., 2016). However, further
601 improvement of our understanding of internal NAO variability and its response to climate change is crucial
602 to future model predictions of winter temperature and precipitation across decadal scales (Smith et al.,
603 2020, Athanasiadis et al., 2020). It is important to note that any effects of NAO are superimposed on those
604 of anthropogenic climate change, potentially alternately masking and enhancing the trends expected
605 under scenarios of climate change (Deser et al., 2017, Iles and Hegerl, 2017). At this point, predicting to
606 what extent anthropogenic climate change may lead to a preferential occurrence of either a positive NAO,
607 resulting in dominating westerlies and subsequently more snow accumulation at Finse, or negative NAO
608 phase, or how NAO-phase amplitude is affected, remains an active field of research.

609 *Scaling up from species to communities and ecosystem processes*

610 The responses of plant and animal communities to environmental change can manifest through changes
611 in species population dynamics and distributions, phenology, and morphological and physiological traits
612 (including underlying genetics) (Bellard et al., 2012). Although individual plant species showed changes in
613 population dynamics in response to environmental manipulations at Finse (Figure 6), we know little about
614 how this affects their distribution at a larger scale. For example, we lack evidence for increasing
615 biodiversity at high elevation such as found in other mountain areas (Steinbauer et al., 2018), and data on
616 whether invasive, lowland species manage to establish in warm or disturbed microsites at Finse such as
617 elsewhere in the alpine (Lembrechts et al., 2018, Lembrechts et al., 2016, Rashid et al., 2021, Pauli et al.,
618 2012). Contrasting species-specific responses to environmental manipulation suggest that there is no one
619 general response to environmental change, which increases the relevance and need of studies at the
620 community-level that show the collective outcome of individual species population dynamics and
621 interactions.

622 Although individual plant species (Klanderud, 2008) and plant community functional composition (van
623 Zuijlen et al. 2021b) responded to experimental warming at Finse, the effect on the *Dryas* heath plant

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

636 Functional traits are a tool to translate taxonomic responses to environmental change into ecological
637 functioning (e.g. Violle et al., 2007). Theoretically, ameliorated environmental conditions should shift
638 plant traits towards those associated with fast returns on investment and acquisitive resource strategies
639 such as increased specific leaf area, and increased tissue nutrient status (Wright et al., 2004). However,
640 studies on primary producer community-level traits in response to experimental warming and across
641 elevation showed little or contrasting responses (Van Zuijlen et al., 2022b, Roos et al., 2019), similar to
642 some other alpine sites (Sundqvist et al., 2013). At the biome-wide scale, environmental drivers were
643 found to structure not only individual plant traits but also trait combinations and trade-offs, which limits
644 the number of successful trait combinations that can persist as environmental conditions change
645 (Bjorkman et al., 2018). As such, communities dominated by long-lived, stress tolerant species (e.g. *D.*
646 *octopetala*) may respond less than communities with larger biological productivity (Hudson and Henry,
647 2010), especially when amelioration of one environmental variable (e.g. temperature) coincides with an
648 increase in other environmental stressors (e.g. summer drought, reduced snow cover). We therefore
649 suggest that the modest community-level trait responses at Finse may be due to the harsh environment
650 at Finse, ensuring stable community compositions, limited establishment of new species, and maintaining
651 the conservative trait strategies of existing plant communities.

652 Plant traits may have afterlife effects (e.g. through litter) that impact ecological processes such as
653 decomposition and ultimately carbon and nutrient cycling (e.g. Cornelissen et al., 2004, Makkonen et al.,
654 2012). In a warmer climate, decomposition rates and nutrient turnover may be expected to increase (see

655 Davidson and Janssens, 2006), but a recent review on decomposition in the alpine showed strong
656 contrasts in responses to environmental factors, although soil moisture generally had a positive effect on
657 decomposition rates (Rawat et al., 2021). Because the experimental warming at Finse and other sites may
658 lower soil moisture (Dabros et al., 2010), any decreases in decomposition rates may in fact not be due to
659 increased temperature but due to low soil and litter moisture. Decomposition and nutrient cycling are
660 complex processes that depend on multiple drivers (litter quality, decomposer communities, and
661 environmental conditions) that act at different scales (Bradford et al., 2017). More research is thus
662 required to fully understand how environmental change may affect decomposition and subsequent
663 processes such as nitrogen cycling and net ecosystem respiration.

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

675 Conclusions and future outlook

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

682 Based on the data included in this synthesis, we conclude that climate at Finse is warming at a moderate
683 rate, with minor effects on growing season length and temperatures to date. Landscape heterogeneity
684 and associated variation in microclimate, including snow dynamics, play an important role in the
685 distribution of species at Finse, and heterogeneity may buffer against the effects of environmental change
686 (Post et al., 2009, Suggitt et al., 2018). Experimental warming has had only marginal effects on the alpine
687 plant communities at Finse. However, soil moisture and ambient warming are known drivers of diversity
688 and functional responses of alpine communities (Elmendorf et al., 2012a, Bjorkman et al., 2018) and the
689 cool temperatures in combination with relatively dry conditions that persist in the *Dryas* heath at Finse
690 may help explain our findings. Nevertheless, warming may still have important effects on individual alpine
691 species' life-history, reproductive output, and phenology and thereby interactions with other species. In
692 contrast to warming, nutrient addition strongly impacts plant and soil arthropod communities at Finse,
693 and its effects are further amplified in combination with warming. Collective work from Finse shows that
694 species interactions involving competition, facilitation, herbivory, and predation are important
695 modulators of responses to environmental change, although this literature is biased towards vascular
696 plants.

697 Considering future predictions of environmental conditions at Finse, our work identifies several lines of
698 further research that will strengthen our understanding of ecosystem structure and functioning. First,
699 precipitation is an axis of environmental change (e.g. Vandvik et al., 2020) left unexplored at Finse so far.
700 As such, the effects of altered precipitation regimes in terms of rain and snow, could be combined with
701 existing manipulations of temperature and nutrient status to uncover possible synergistic effects on alpine
702 communities. Further, the work summarized here assumes constant changes in environmental conditions,
703 neglecting the potentially large ecological effects that may accompany episodic or extreme climatic events
704 such as drought. Although the significance of nutrient manipulations at Finse is on par with conclusions

705 from other alpine sites (Bowman et al., 2015, Bowman et al., 2018), it is unknown to what extent the
706 addition of fertilizer accurately simulates natural pathways of altered nutrient availability. Moreover, we
707 lack understanding of interactions between above and belowground (i.e. plant roots, soil fungi, microbes,
708 Metazoa) components of the ecosystem, and how different functional components *sensu* Strimbeck et al.
709 (2019) affect ecosystem carbon and nutrient fluxes. Finally, the formulation and quantification of
710 threshold-levels at which environmental changes irreversibly affect the alpine ecosystem will benefit
711 management goals for biodiversity hotspots such as the *Dryas* heath at Finse.

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721 Competing interest statement

722 The authors declare there are no competing interests.

723 Data availability statement

724 Data will be made available upon acceptance of this manuscript at <https://dataverse.no/dataverse/nmbu>.

725

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1247

1248 Figure captions

1249 Figure 1.

1250 Map of the Finse area showing the sites of the 80 studies included in this synthesis. Each unique study
1251 location is indicated with a number, which refers to Supplementary Table S1. One central coordinate was
1252 used for studies that included multiple sites close to each other. Location 6 includes the studies that do
1253 not refer to any specific study site and location 19 refers to the main ITEX-site at Mt. Sanddalsnuten. The
1254 circle size (surface area) of each pie chart is relative to the number of studies performed at each site, while
1255 the colors indicate the relative representation of study topics. The map was created with ArcGIS Pro v2.5.0
1256 (Esri, 2020) using a standard background map.

1257 Figure 2.

1258 Timeseries of annual (a); winter: December-February (b); spring: March-May (c); summer: June-August
1259 (d); and autumn: September-November (e) temperatures at the Finse (1969-1994) and Finsevatn (2003-
1260 2020) weather station. Annual and seasonal temperatures where at least one month of interpolated data
1261 from the SeNorge database were used are indicated with open circles. Closed circles indicate that data
1262 are entirely based on station observations. Dashed lines indicate the 1970-1990 average for the respective
1263 season, while dotted lines show a smoothed 5-year rolling average. Trendlines (solid) were calculated
1264 from a simple linear model, and shaded areas indicate a 95% CI. Note that y-axis scales differ between
1265 panels.

1266 Figure 3.

1267 Day of the year when the growing season starts (circles) and ends (triangles), using a 0 °C (blue) and 5 °C
1268 (orange) threshold to define the growing season (a). The length of the 0 °C and 5 °C growing season in
1269 days (b). Accumulated thawing degree days (heat sum with 0 °C base temperature) and growing degree
1270 days (heat sum with 5 °C base temperature) (c). The number of days with minimum temperatures below
1271 freezing point during the 0 °C and 5 °C growing seasons (d). Data were calculated from daily temperature
1272 (2 m), measured at the Finse (1970-1994) and Finsevatn (2003 – present) weather stations. Shaded areas
1273 indicate 95% confidence intervals. Solid lines denote significant trends ($p < 0.05$).

1274 **Figure 4.**

1275 Maximum recorded snow depth at the Finse weather station (1970-1994) versus winter (December-
1276 March) North Atlantic Oscillation (NAO) index (a). Colors denote average temperatures over the same
1277 period. Winters with a predominantly positive NAO phase accumulate a significantly deeper snowpack
1278 (b).

1279 **Figure 5.**

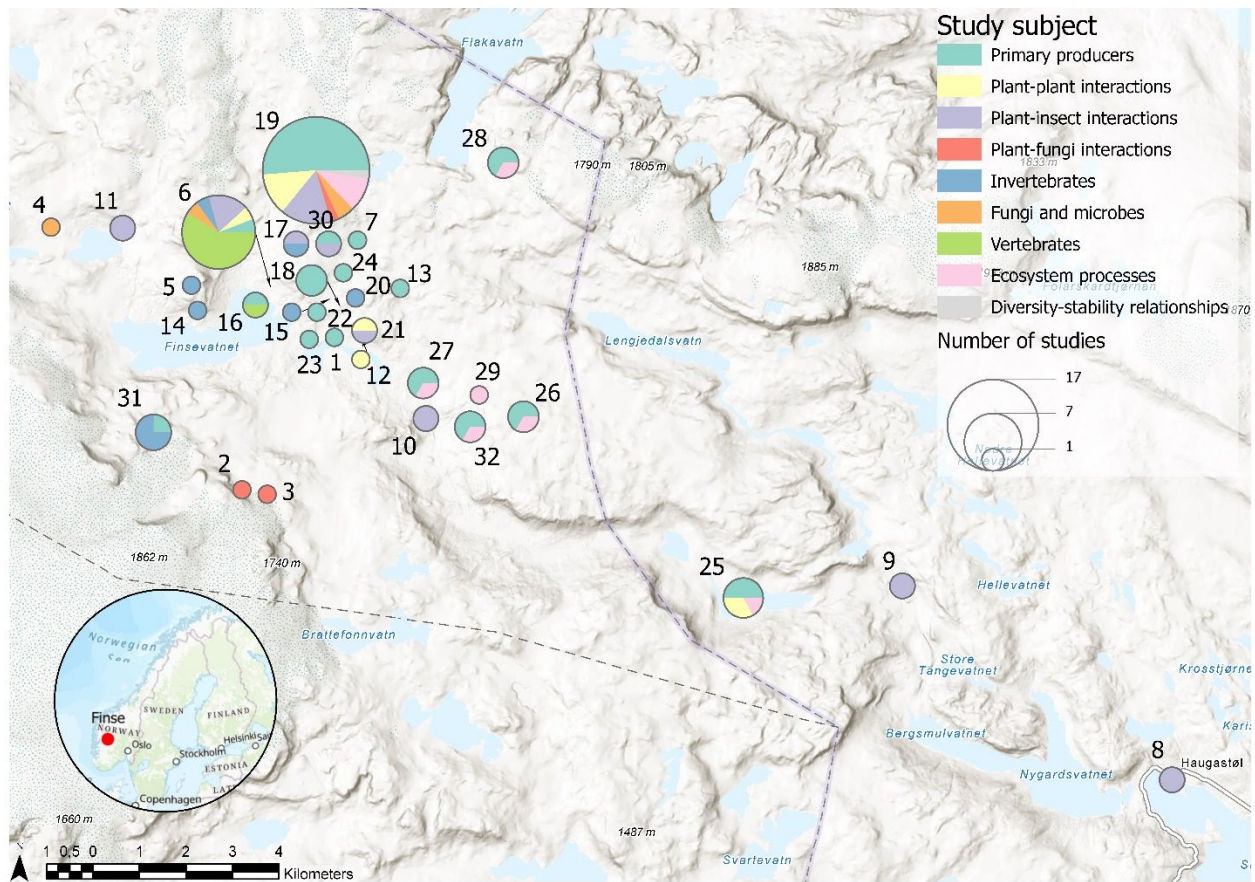
1280 The number of ecological studies (80) performed at Finse per topic (a) and experimental design (b)
1281 included in this synthesis. A study can be assigned to multiple topics or experimental designs. Here,
1282 *Environmental manipulation* includes experiments where temperature, nutrient availability or other
1283 abiotic conditions were altered and compared to control sites. *Environmental gradient* is used in its
1284 broadest sense and includes traditional gradients in environment, including elevation, the use of
1285 contrasting sites, as well as variations in microclimatic conditions across space or time. *Observational*
1286 studies monitor species presence, performance, and behavior *in situ*, across time and space. *Successional*
1287 *gradient* includes studies performed (across different successional stages) at glacial forelands. In
1288 *community manipulations* one or more species were actively removed or added to an ecological
1289 community, while in *individual manipulations* individual organisms were manipulated to investigate their
1290 performance. *Transplant* experiments are those where organisms or materials from a common
1291 environment are actively transplanted across sites with different environmental conditions. Vice versa,
1292 *common garden* comprises those studies where one or more species or materials were moved from their
1293 native environments into a common environment. *Cafeteria trials* offer a variety of food items to
1294 organisms to establish their dietary preferences.

1295 **Figure 6.**

1296 Graphical summary of the observed climate and climate trends at Finse, and of the ecological responses
1297 to experimental and ambient environmental change at Finse over the past three decades. The top
1298 segment "observed climate" refers to the observed trends and dynamics of the climate at Finse. The right
1299 segment "warming response" summarizes the observed responses individual species, communities, and
1300 ecological processes to both experimental and ambient climate change. The left segment "nutrient
1301 addition response" summarizes the observed responses of species, communities, and ecological
1302 processes to experimental nutrient addition.

1303 Figures

1304 Figure 1.



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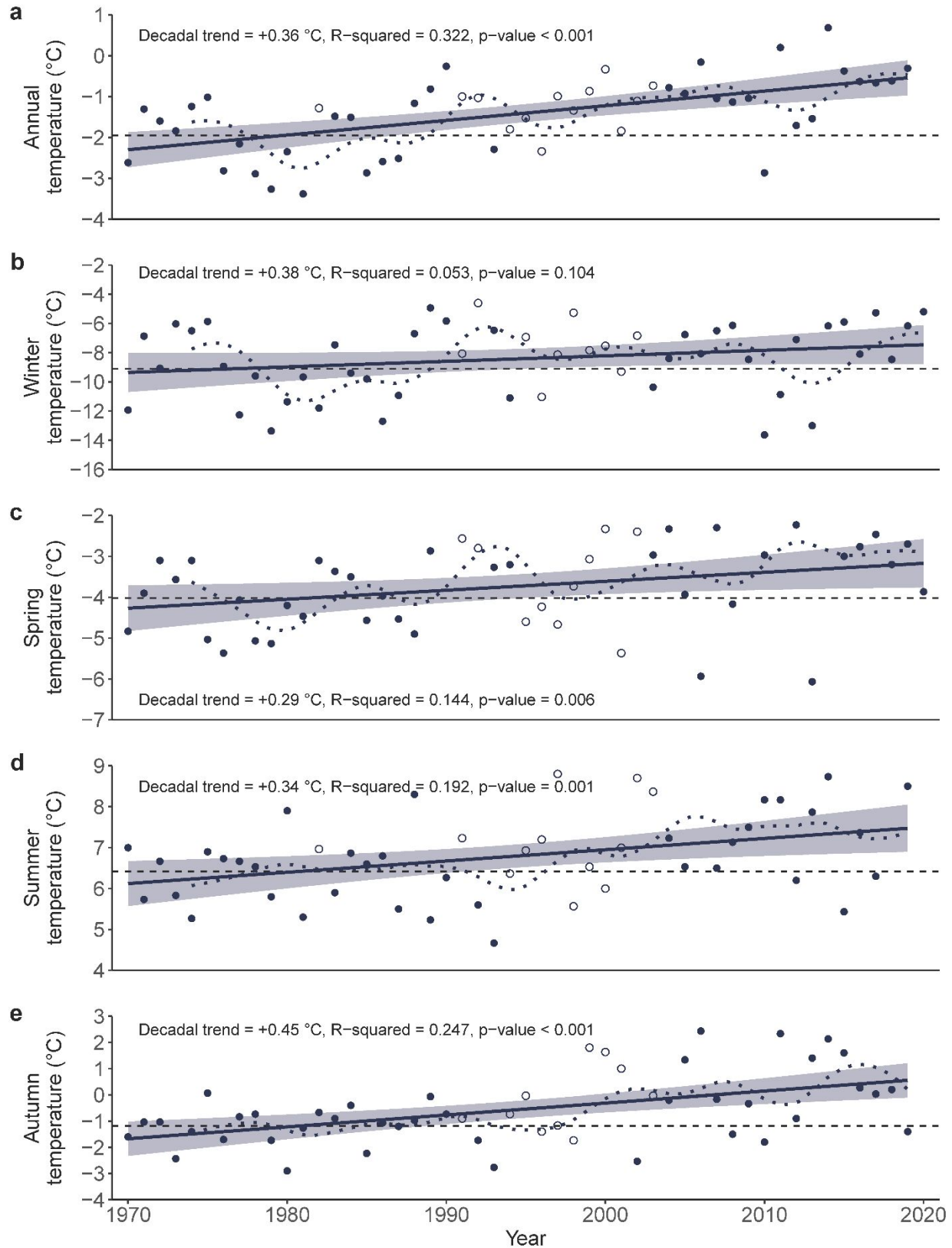
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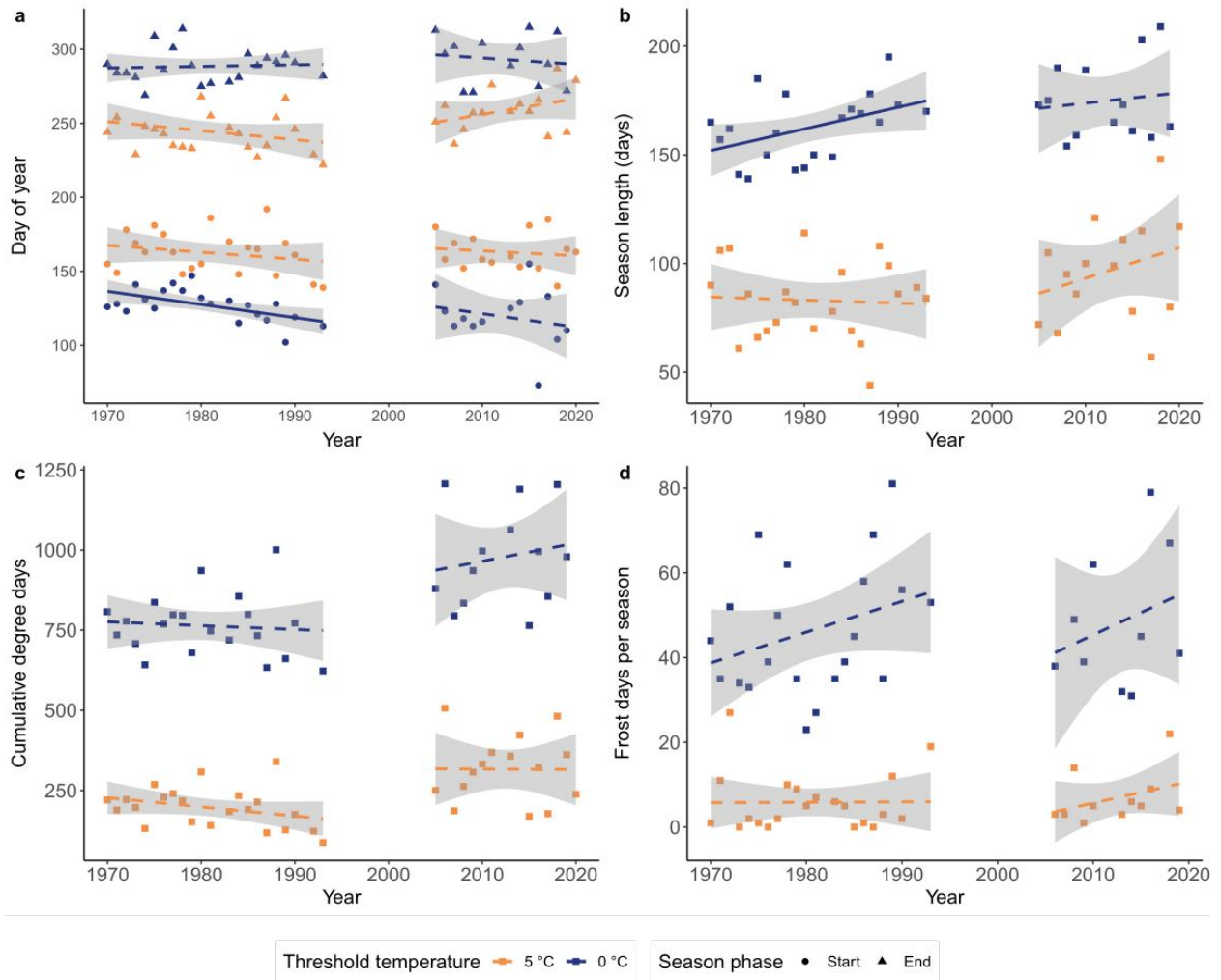
1311 **Figure 2.**



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1313 Figure 3.

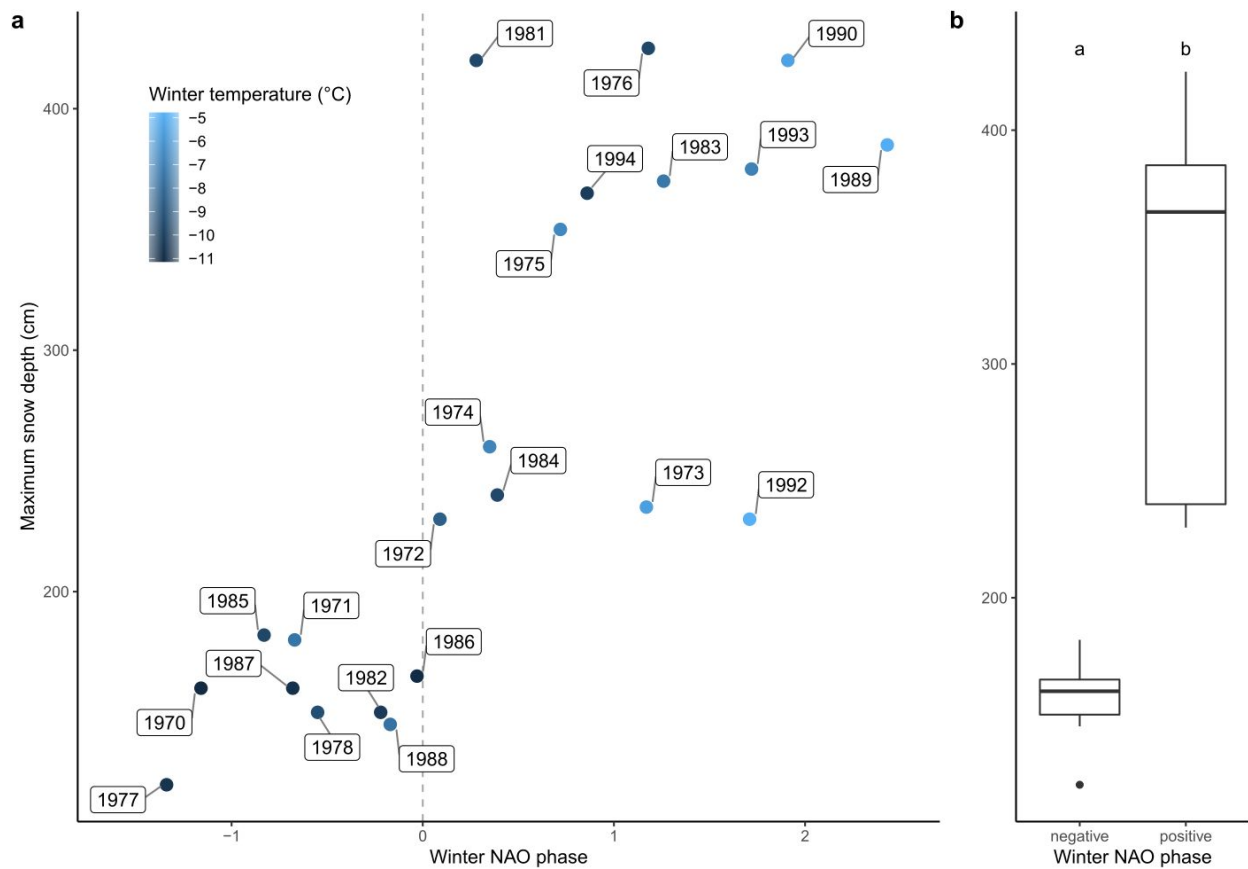
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1317 **Figure 4.**



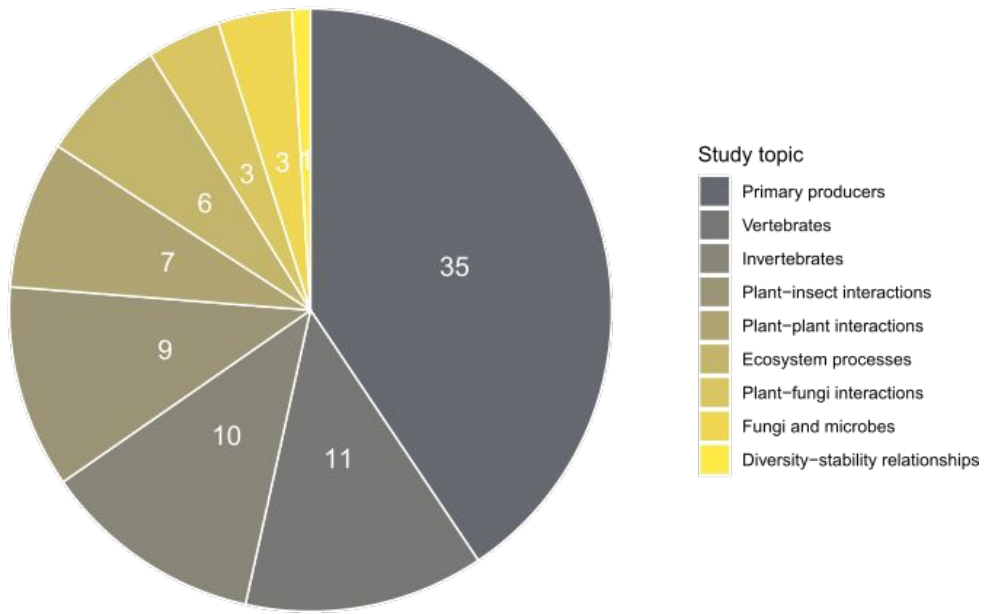
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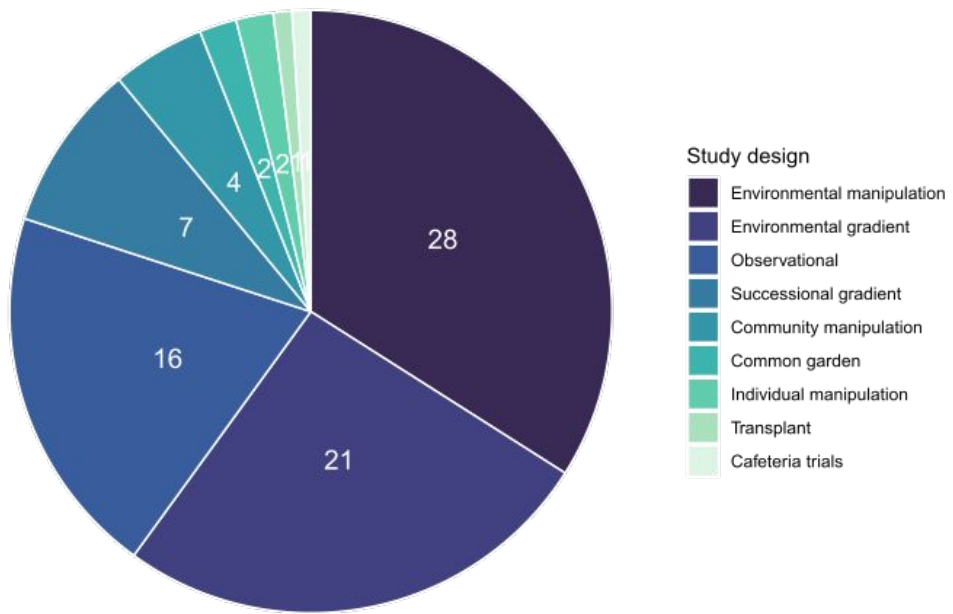
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1320 **Figure 5.**

a

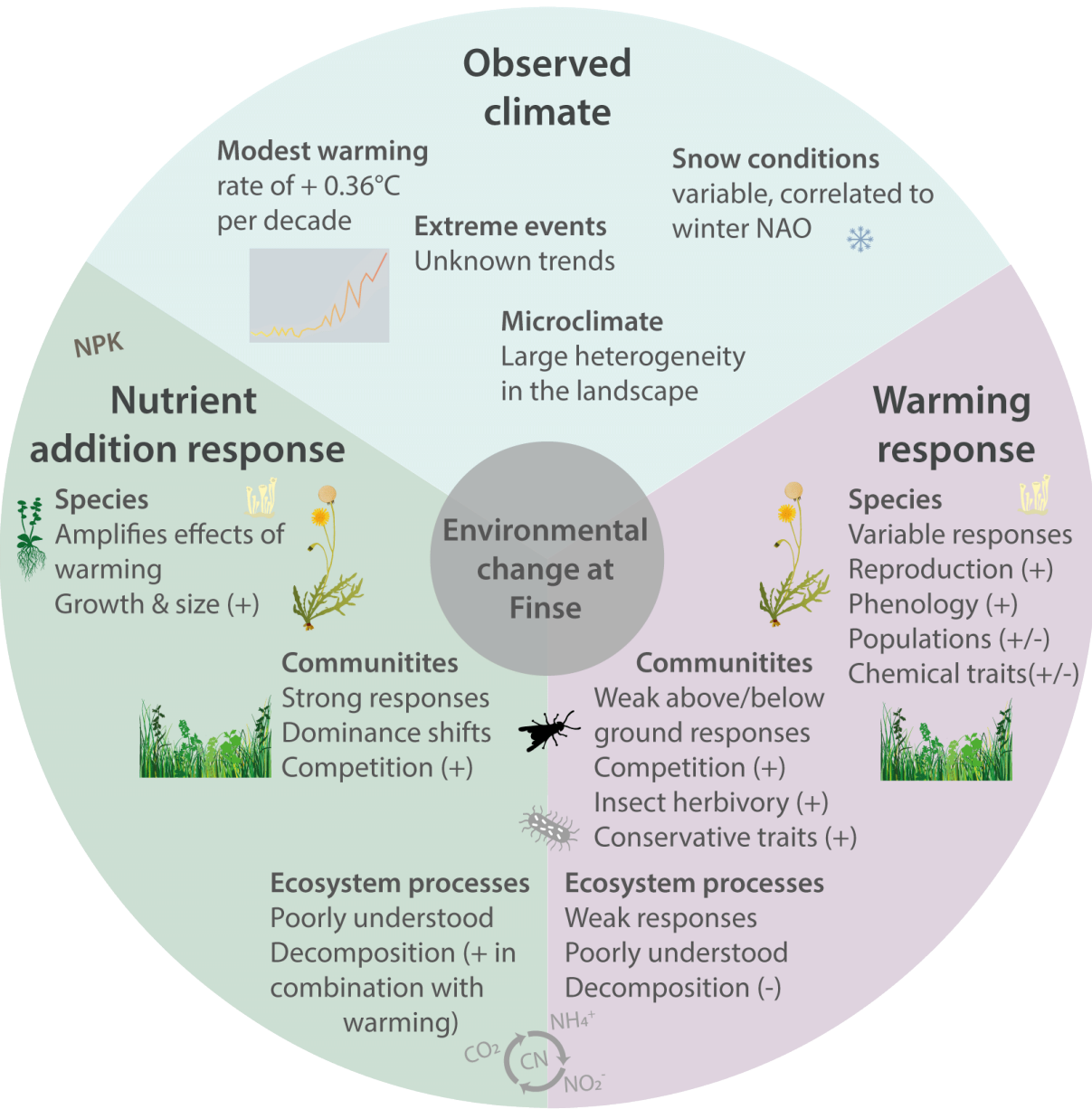


b



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1322 Figure 6.



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