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Short communication

Widespread plant species temporal variation along environmental and microclimate gradients in Norwegian mountains in a climate change context

Sølvi Wehn[1,2], **Ketil Isaksen**[3] **and Line Johansen**[1]

[1]Norwegian Institute of Bioeconomy Research (NIBIO), Trondheim, Norway
[2]Multiconsult, Trondheim, Norway
[3]Norwegian Meteorological Institute, Oslo, Norway

Correspondence: Sølvi Wehn (sw@multiconsult.no)

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The effect of climate change on mountain vegetation is influenced by environmental factors and site effects. To monitor the effect of climate change we therefore need to understand species' sensitivity to microclimate and environmental gradients. The objective of this study is to study widespread plant species' temporal and spatial variation along environmental and microclimate gradients in Norwegian mountains along a coast–inland gradient. Occurrence and abundance of plant species were surveyed in 110 study plots in four mountains at two points in time, seven years apart. Of the 222 plant species registered, *Salix herbacea*, *Phyllodoce caerulea*, *Carex bigelowii*, *Juncus trifidus*, *Vaccinium myrtillus*, *Avenella flexuosa*, and *Empetrum nigrum* were widespread across all mountains. These species responded differently to environmental and microclimate gradients, and abundance data were more sensitive than occurrence data. During the short time span we observed some indications of response which might support the assumption that boreal species outcompete alpine species in the forest transition zone, but our data do not indicate this effect at higher altitudes. Monitoring of climate change in mountains needs to include plots along environmental and microclimate gradients as well as an abundance of a set of widespread plant species that represent regional, local environmental, and climate gradients. However, when monitoring perennial plant species, the need for long-term monitoring projects is high because such species develop slowly over several decades.

Keywords: alpine vegetation change, *Avenella flexuosa*, *Carex bigelowii*, climate change, *Empetrum nigrum*, GLORIA (Global Observation Research Initiative in Alpine Environments), *Juncus trifidus*, microclimate, *Phyllodoce caerulea*, *Salix herbacea*, soil temperature, *Vaccinium myrtillus*

Introduction

Global climate change is among one of the largest drivers of biodiversity loss (Verrall and Pickering 2020) and alpine environments are particularly vulnerable

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(Nagy and Grabherr 2009). Alpine environments inhabit unique ecosystems where plant species have adapted to a harsh climate (Billings 1974) defined by soil conditions (e.g. soil temperature) and formed by small-scale topography (Winkler et al. 2019).

Environmental and microclimatic drivers vary along the altitudinal gradient and altitudinal shifts as responses to climate change are driven by the species' distribution across geographic space (Wang et al. 2020, Zu et al 2021). Similarly, alpine plant species communities' responses to climate change vary from site to site, both at regional and local scale (Winkler et al. 2019). There are different responses to climate change across mountains along continental as well as local gradients, such as the snow cover exposure gradient (Kudo et al. 2010, Gottfried et al. 2012). The relationship between microclimate and alpine vegetation, however, remains understudied (Ohler et al. 2020) which highlights the importance of linking plant species with the spatiotemporal and abiotic variation in a climate change context.

Long-term ecological monitoring is highly important to increase our understanding of the complex bioclimatic dynamics in alpine ecosystems, particularly in light of the ongoing climate change (Verrall and Pickering 2020). Ecological monitoring is often divided into comprehensive monitoring of as many species as possible or monitoring of a single species (Lindenmayer and Likens 2010). The advantage of using a single species is that it requires less sampling effort and contributes to more effective sampling compared to more comprehensive surveys.

Vascular plants are widely used for monitoring in climate impact studies (Corlett and Wescott 2013). However, as Winkler et al. (2019) imply, there are different responses among species to climate change, and single species' responses to climate change can vary along different environmental and microclimatic conditions. This means that the selection of species for climate change monitoring must be based on knowledge of their distribution as well as sensitivity to environmental change.

Widespread species, in contrast to rare species, require less species identification skills of the observer and contribute to less observer bias and effective sampling across environmental gradients (Higa et al. 2013). Furthermore, by monitoring widespread species, it is more cost-effective to access a large amount of data and consequently develop more robust models to identify species sensitivity to climate change.

Some widespread species in mountains can be more generalists compared to others that have a narrower distribution niche linked to alpine environments only. Following the argument of Nagy and Grabherr (2009), the assumption is that those species associated with alpine environments only are the most vulnerable to climate change.

The objective of this paper is to identify widespread plant species in Norwegian mountains that are sensitive to ecological and microclimatic variation in mountains, and then to study whether these plant species show spatial and temporal variation during a period of seven years.

Material and methods

Study sites and plots

The study sites were four mountains along a coast–inland gradient in central Norway: the coastal mountain Stortussen, the inner fiord mountain Kaldfonna, the mountain Kolla at the main watershed at Dovrefjell, and the easternmost mountain Tron (Fig. 1, Supporting information). Study plots were distributed in a systematic way through stratification of mountain slopes from below the forest line upwards to the summit in vertical belts on each mountain. In each belt, 1–3 plots were located, covering the local snow cover duration gradient. Whenever possible, vertical belts were in different aspects. In all mountains, and in all plots, sheep graze during summer. The grazing pressure had not changed significantly during the period of the study. Hence, we assume that if vegetation changes are observed, this is not due to changed grazing pressure.

During 2009–2012 we established in total 110 permanent study plots (10 × 10 m) in the study sites, one site each year. The study plot coordinates were recorded with GPS (± 5 m), marked with stones and nails, and identified with photos. The study plots were established as part of a project aiming to monitor abiotic and biotic factors in Norwegian mountains in relation to predicted climate changes with methods derived from the worldwide long-term observation network Global Observation Research Initiative in Alpine Environments (GLORIA; Grabherr et al. 2000, GLORIA 2001–2024, The Norwegian Environmental Agency 2023).

Data survey and analyses

In each study plot, we recorded occurrence (presence/absence) and abundance classes of all vascular plant species. Abundances were classified in five classes: 0 (absence), 0.0001% (very rare; one or a few small individuals), 0.0005% (rare; some individuals at several locations), 1% (scattered; widespread within the section), 5% (common; occurring frequently and widespread within the section), and 25% (dominant; very abundant). Data were sampled twice at an interval of seven years (Supporting information). The plant species' distributional range along temperature and vegetation types that reflect snow cover gradients were obtained from Lid and Lid (2005).

Meter above forest line (m a.f.l.) was used to represent the altitudinal gradient. Forest line was estimated based on visual interpretation of aerial photographs using ArcGis Pro (Esri), and m a.f.l. was calculated based on a digital terrain model (dtm) provided by the Norwegian Mapping Authority. The coast–inland gradient was represented by a categorical predictor with four levels (the four sites (Fig. 1)).

Soil temperature was monitored in 106 of the study plots during the study period (Supporting information) by using soil temperature data loggers at ca 5 cm depths placed in the centre of the study plots if possible. Based on the soil temperature data, three low multi-collinearity microclimate

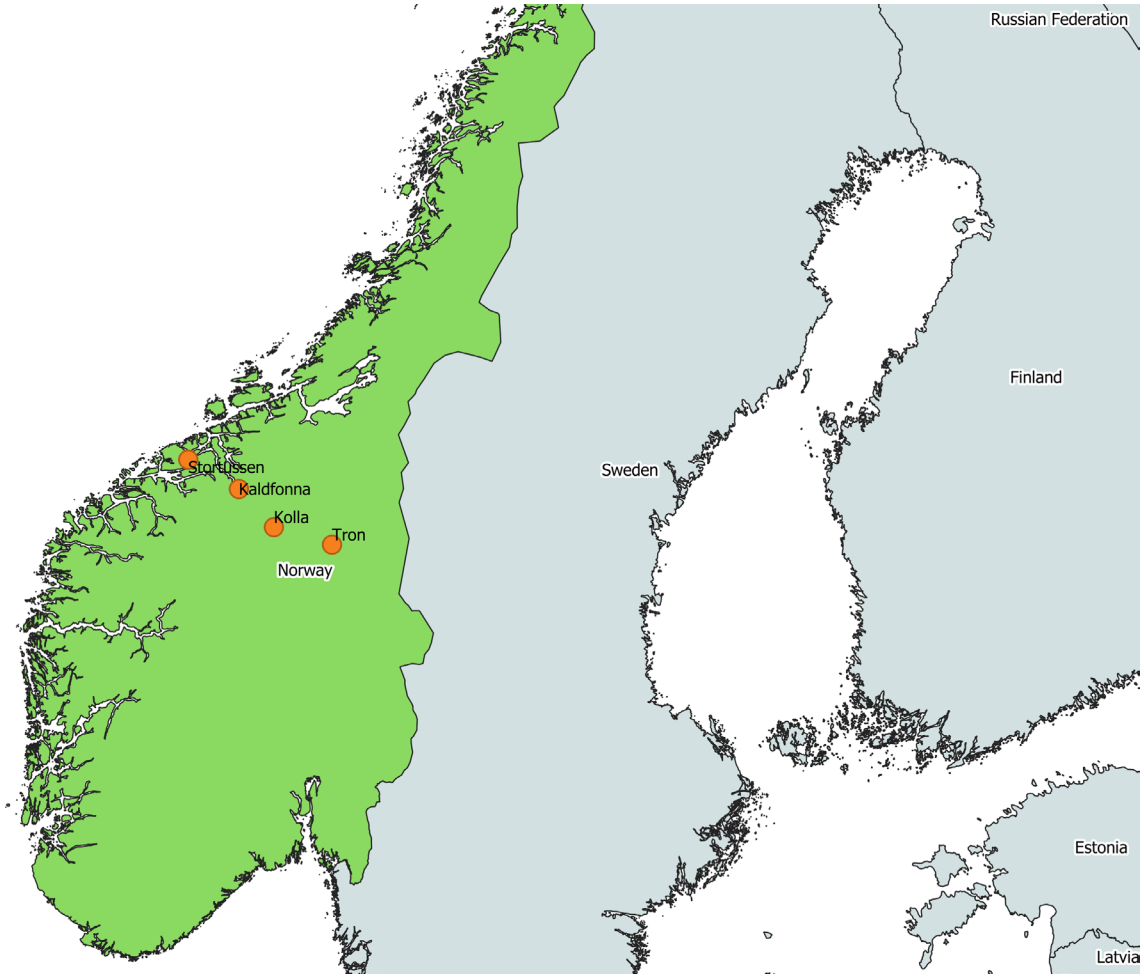


Figure 1. The study sites were four mountains along a coast–inland gradient in central Norway.

indicators relevant for studying climate change were calculated for each study plot: growing season temperature (average temperatures for the period where the mean soil temperature is > 5°C), winter temperature (mean temperatures for the period December–February), and start of growing season (the period when mean daily soil temperature is > 5°C). The microclimate indicators were calculated as averages during the period sampled (the period of soil temperature data for each mountain site in Supporting information). This means that, for one study plot, one value of each microclimate indicator represents both survey years. To achieve microclimate indicators that are representative for the conditions the long-lived plant species are facing, soil temperature measurements outside the vegetation survey period were also included as data to calculate the microclimate indicators.

We calculated the number of plots in which each species occurred to detect widespread species. We defined a species to be widespread if it occurred in 60% or more of all surveyed study plots and tested spatial variation of these widespread species along environmental gradients (m a.f.l., coast–inland) and microclimate gradients (growing season temperature, winter temperature, start of growing season). For each of the species, we then tested temporal variation in occurrence and abundance during seven years. Discussion of the results is based on the widespread species' distributional range.

For all tests, we developed generalized linear mixed models (glmer) with binomial distribution for occurrence data and negative binomial distribution for abundance data due to overdispersion. Study plot id was included as a random effect term in all models. For each species potential polynomial relationships with altitude (m a.f.l.2) were explored by plotting polynomial regression lines. If significant time effects were found, we tested if time effects varied along the explanatory variables (each environmental and microclimatic gradient) by including interactions between each of the explanatory variables and survey number (year); that is, we investigated if the change between survey year for one gradient, varied along the gradient.

Statistical tests were performed in R ver. 3.6.0 (www.r-project.org). The glmer were developed using the lme4-library. Plots with polynomial regression lines were developed by using the 'ggplot' function *stat_smooth*. To assess model fit, a forward selection procedure was performed by using likelihood ratio tests to determine the contribution of each

main effect and their interaction. By using likelihood ratio tests simpler models were compared with models that also included the explanatory variables. For each species and for each environmental and microclimate gradient, the procedure was 1) comparing an intercept-only model with a model that included one of the gradients or survey numbers, 2) if survey number was significant, comparing a model that included survey number only with a model that also included the interaction between the survey number and one of the environmental or microclimate gradients. The models were checked for overdispersion using the blmeco-library.

Results and discussion

Of the 222 vascular plant species observed, we identified seven species (*S. herbacea*, *P. caerulea*, *C. bigelowi*, *J. trifidus*, *V. myrtillus*, *A. flexuosa*, *E. nigrum*) that were widely distributed across all four mountains (Supporting information).

Occurrence and abundance of all seven species responded to one or more of the environmental and microclimate gradients investigated (Table 1, Supporting information). Due to this sensitivity to ecological and microclimate variation, we assumed that these seven species are sensitive to climate change. Our assumption is backed up by earlier studies that have shown that *C. bigelowii*, *V. myrtillus*, and *E. nigrum* are favoured by warmer climates (Stenström and Jónsdóttir 1997, Rixen et al. 2010, Kapfer and Popova 2021) and that *S. herbacea* responds both to temperature and precipitation changes (Phulara et al. 2022). Furthermore, several of the species (e.g. *A. flexuosa*, *V. myrtillus*, *P. caerulea*, *J. trifidus*, *and E. nigrum*) are reported to have shown changed distributions due to climate change (Klanderud and Birks 2003, Kapfer and Popova 2021).

The seven species have different distributions along the temperature gradient and between mountain vegetation types (Table 1) and our results show that they have different responses to environmental and microclimate gradients. This illustrates the need for monitoring of multiple species to capture the total effect of climate change. By monitoring a set of species that represent the variation along multiple gradients, the design is more robust to temporal and spatial variation compared to monitoring of one species only. Our results also indicate that abundance data better detect short time changes in plant species communities compared to occurrence data only.

Six of the seven species had no change in occurrence during seven years (Table 1), while all species showed changed abundances (Supporting information).

Generally, abundance of the species was higher in the second survey. Mostly, the increase was in the plots where the species already had large abundances the first year of monitoring. There might be a risk that the abundance data are biased by individual differences in estimating abundance, as different persons were doing the surveys between years (discussed in Futschik et al. 2020, for example). However, we trust the results as the data show no consistent increase in abundance between the species nor along the environmental and microclimate gradients.

The results that we discuss here can be explained by the species' distributional ranges (Table 1). The nemoral to mid-alpine species (boreal species) were widely present and dominant in the most coastal mountains, and boreonemoral to polar desert species (alpine species) were more dominant in the inland mountains (Supporting information). Elevation range shifts of alpine plant species caused by global warming has been observed in several mountain regions across the world (Scandes: Løkken et al. 2020, Andes Mountains: Sklenář et al. 2021, Sichuan, China: Zu et al. 2021). Most common elevation range shifts are upward elevation movement of plant species (Løkken et al. 2020, Sklenář et al. 2021, Zu et al. 2021), but downslope shifts have also been reported (Zu et al. 2021). The trends shown in our study partly support the assumptions that lowland and low alpine species have the potential to outcompete higher alpine species, as our data show a small increase in abundance in a boreal species *V. myrtillus* in the forest-alpine transition zone. But our data also show that the higher-altitude species *J. trifididus*, *C. bigelowii*, and *S. herbacea* had increased in abundance in higher altitudes (approximately 500 m a.f.l.).

The time effect varied between mountains for all species and along one or more of the microclimate gradients for four of the seven species (Table 1, Supporting information). Like Gottfried et al. (2012) and Winkler et al. (2019), we observed different short time temporal variation at species level between sites.

Hanssen-Bauer et al. (2017) predict a higher increase in the number of warm days and annual precipitation in inland areas compared to at the coast. We therefore expected our data to show signs of species transitions in the more inland mountains, which indicate that environments become more similar across the coast–inland gradient. We were, however, not able to show this with our data as the boreal species *A. flexuosa* increased the most in abundance at the most coastal mountain, and the alpine species (*C. bigelowii* and *S. herbacea*) increased the most in the most inland mountains. However, *E. nigrum*, a species that is reported to have increased in number of occurrences across a subarctic peninsula (Kapfer and Popova 2021) shows increased abundances in all mountains but one. The decline of *E. nigrum* in one of the mountains may be due to drought, as the species is known to be sensitive to warmer conditions and drought during winter (Dobbert et al. 2021).

Our results do not show the expected response to climate warming where boreal/lower alpine species replace higher altitude species (as shown by Klanderud and Birks 2003, for example), as the high-altitude species *C. bigelowii* had increased in abundance in the lowest winter temperatures and the most alpine species (*S. herbacea)* had increased in abundance in the lowest growing season temperatures (Supporting information).

Liberati et al. (2019) report that snowbeds are becoming dryer because of earlier snowmelt. Species adapted to a short growing season, but moist environment, might consequently

Table 1. The seven most widespread plant species across four mountains along a coast–inland gradient in central Norway. The species are sorted according to the species' distributional range along the temperature gradient and vegetation types that reflect the snow cover gradient (Lid and Lid 2005). Number of observations: number of 100 m^2 plots in which the species occurred; total number of plots are 220 (includes both years). The three last columns show results of the statistical modelling performed (test statistics are shown in Supporting information). Dependent variables: occurrence and abundance. Explanatory variables: environmental and microclimate gradients. Environmental gradients were mountain: four mountains along the coast–inland gradient in central Norway, and altitude: m a.f.l.: meter above forest line. Microclimate gradients were growing season temperature: average temperatures for the period when mean soil temperature is > 5°C, winter temperature: mean temperatures for December–February, and start of growing season: mean daily soil temperature is > 5°C.

	Distributional range					
Species	Temperature gradient	Vegetation type	Number of observations	Spatial variation along:	Change during seven years	Different changes between years along
Salix herbacea	Mid boreal to polar desert	Snowbed	141	*Occurrence:* mountains, altitudes, winter temperatures, start of growing seasons *Abundance:* altitudes, winter temperature, start of growing seasons	*Occurrence*: no *Abundance*: yes	*Abundance:* mountains, growing season temperatures
Phyllodoce caerulea	Mid-boreal to polar desert	Heath and forest	131	*Occurrence:* mountains, altitudes, winter temperatures, start of growing seasons *Abundance:* altitudes	*Occurrence:* yes *Abundance:* yes	*Abundance:* mountains
Carex bigelowii	Boreonemoral to polar desert	Ridge, heath, snowbed, mire, grassland	152	*Occurrence:* mountains, altitudes *Abundance:* mountains, altitudes, growing season temperatures, winter temperatures, start of growing seasons	*Occurrence:* no *Abundance:* yes	*Abundance:* mountains, winter temperatures
Juncus trifidus	Boreonemoral to high alpine	Ridge, snowbed	133	*Occurrence*: mountains, altitudes *Abundance:* mountains, altitudes, winter temperatures	*Occurrence:* no *Abundance:* yes	
Vaccinium myrtillus	Nemoral to mid-alpine	Forest, mire, heath, leeside	134	*Occurrence*: mountains, altitudes, growing season temperatures, winter temperatures *Abundance:* mountains, altitudes, growing season temperatures, winter temperatures, start of growing seasons	*Occurrence:* no *Abundance:* yes	*Abundance:* mountains
Avenella flexuosa	Nemoral to mid- alpine	Forest, heath, dry grassland	135	*Occurrence*: mountains, altitudes, growing season temperatures, winter temperatures *Abundance:* mountains, altitudes, growing season temperatures, winter temperatures, start of growing seasons	*Occurrence:* no *Abundance:* yes	*Abundance:* mountains, growing season temperatures
Empetrum nigrum	Nemoral to mid- alpine	Forest, mire, heath	170	*Occurrence*: altitudes *Abundance:* altitudes, winter temperatures	*Occurrence:* no *Abundance:* yes	*Abundance:* mountains, winter temperatures

lose in the competition with superior species that survive in drier environments. The start of the growing season did not influence the time effect on abundance of either of the widespread species, hence we cannot conclude that the snowbeds have become drier. The growing season temperature, on the other hand, showed a little negative influence in the highest temperatures on the snowbed species *S. herbacea*. We therefore argue that if the growing season starts earlier, more boreal species that prefer heaths and leeside vegetation will outcompete alpine species and species that prefer snowbeds, because higher temperatures lead to a drier environment.

Concluding remarks

Our study shows the need for monitoring a set of species that represent both regional and local environmental and climatic gradients in sites along a wide geographic range to

fully disentangle vegetation response to climate change. But, more importantly, our results show the need for long-term monitoring. A time span of seven years is not enough to fully understand the dynamics of alpine vegetation response to climate change. The effects of climate changes on perennial plant species develop slowly over several decades, hence there is an urgent need for long-term monitoring projects.

During the short time span we observed some indications of response, such as a slight increase in abundance in *V. myrtillus* at lower altitudes in the forest alpine transition zone, which might support the assumption that boreal species outcompete alpine species in the forest transition zone, but our data do not indicate this effect at higher altitudes. At higher altitudes more alpine species such as *S. herbaceae*, *C. bigelowii*, and *J. trifudus* have increased in abundance.

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Author contributions

Sølvi Wehn: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ketil Isaksen**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting). **Line Johansen**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.7h44j102b (Wehn and Isaksen 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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