Riding the elevator to extinction: Disjunct arctic-alpine plants of open habitats decline as their more competitive neighbours expand

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ABSTRACT

Major displacement of arctic-alpine species towards higher elevations and latitudes is anticipated under climate warming. Disjunct plant populations persisting on mountains at the limits of their species' distributions may have a reduced capacity for migration, and therefore offer a particularly sensitive indication of climate change effects. The flora of Scotland's mountains is of international significance because it contains populations of climate relicts which are isolated geographically and located at the rear edge of their global range. We used a unique long-term monitoring dataset recording vegetation change at a mountain outpost site in the Scottish Highlands to identify divergent population trends in ten rare plant species over the last 30 years. Three arctic-alpine specialists (*Sagina nivalis*, *Sabulina rubella* and *Saxifraga cernua*) have suffered severe declines of over 50 % of their population size since the mid-1990s, and have been extirpated at their lowest altitude locations. These species are undergoing elevational range contractions and *Sagina nivalis* is now considered Endangered in Britain. Their open, gravelly snowbed habitats have been affected by vegetation encroachment, landslip and rockfalls. Population changes across all species studied were also significantly related to altitude. Species with stable or increasing population sizes occur at lower altitudes, are taller and have less reliance on sparsely vegetated habitats. These results can be contextualised within broad trends of thermophilization, biotic homogenization, mountain greening and snow cover declines. Our work demonstrates that disjunct low-latitude arctic-alpine plant populations already situated at maximum local elevational gradients could face "mountaintop extinction", with implications for the conservation of regional biodiversity.

1. Introduction

The ongoing impacts of climate change on the distribution and preservation of biodiversity are matters of global significance (Habel et al., 2010; Bellard et al., 2012; Pettorelli et al., 2021; Habibullah et al., 2022). Rising temperatures linked to anthropogenic greenhouse gas emissions are causing worldwide geographical displacement of the climates to which species are adapted (IPCC, 2014, 2022). Climate-driven range shifts and extinctions have implications for ecosystem structure and function, with potential impacts on carbon sequestration, pathogen spread, food security and human wellbeing (Pecl et al., 2017; Díaz et al., 2019; Arneth et al., 2020).

Species are vulnerable to extinction linked to climate change if they cannot adapt to new climatic conditions or migrate to more suitable regions (Parmesan, 2006). Constraints on distributional shifts include dispersal obstacles, competitive interactions, slow migration speeds and low habitat availability (Feeley and Silman, 2010; Bertrand et al., 2011; Ameztegui et al., 2016; Fricke et al., 2022). These barriers have particular relevance to climate relicts; defined as disjunct populations restricted geographically to islands of suitable habitat within an inhospitable climate (Habel et al., 2010; Hampe and Jump, 2011; Fragnière et al., 2020).

Major distributional displacement of species towards higher elevations and latitudes is anticipated under warming scenarios (Sturm et al., 2001; Root et al., 2003; Parmesan, 2006; Lenoir et al., 2008; Jump et al., 2009; Chen et al., 2011; Engler et al., 2011; Morueta-Holme et al., 2015; Rogora et al., 2018; Steinbauer et al., 2018; Niskanen et al., 2019). Mountain systems are key biogeographic components of ecological,

climatic, hydrological and socioeconomic value, but are particularly sensitive to environmental perturbation (Körner, 2003; Viviroli and Weingartner, 2004; Wielgolaski et al., 2017). Many marginal montane plants grow slowly and reproduce predominantly vegetatively, and so are less likely to disperse into new climatically suitable locations in the short timescales required to keep pace with rapid global change (Dullinger et al., 2004; Alexander et al., 2018). Disjunct arctic-alpine plant populations that have persisted on isolated mountain outpost sites at the limits of their species' distributions are climate relicts that offer a particularly sensitive indication of climate change effects (Lesica and McCune, 2004; Kougioumoutzis et al., 2021).

Mountain vegetation is being studied worldwide to provide key knowledge on the ongoing risks to biodiversity caused by climate change (Grabherr et al., 1994; Grace et al., 2002; Hassol, 2004; Colwell et al., 2008; Holtmeier and Broll, 2010; Jump et al., 2012; Steinbauer et al., 2018). However, methodological difficulties and low research effort have resulted in less evidence of range retraction at the low-latitude margins (the rear edge) of species' distributions and therefore a disparity between observations and predictions (Jump et al., 2009; Vilà-Cabrera et al., 2019). An improved understanding of changing trends in disjunct montane plant populations and the fate of low-latitude climate relicts has major implications for conservation biology (Chapman, 2013; Abeli et al., 2018). High altitude regions can contain significant habitat heterogeneity and be disproportionately important for their biodiversity (Lomolino, 2001; Körner, 2003; Nagy and Grabherr, 2009; Greenwood and Jump, 2014), while rear edge populations can exhibit rich genetic diversity and distinct local adaptations in comparison to the range core (Hampe and Petit, 2005; Provan and Maggs, 2012; Rehm et al., 2015).

Investigating which groups of arctic-alpine plants are most at risk on mountain outpost sites will be critical for developing targeted conservation action to preserve valuable genetic resources and evolutionary potential during global change. Further research is required to identify the key traits and habitat types of diminishing species which are facing uphill distributional shifts or range contractions (Stöckli et al., 2011). A multi-taxon approach along elevational gradients will assist with disentangling complex community diversity patterns which are significantly influenced by localised variations in altitude and topography (McCain and Grytnes, 2010; Graae et al., 2018; O'Sullivan et al., 2020; Di Nuzzo et al., 2021).

Long-term population monitoring is essential for detecting changing trends, evaluating threats and informing conservation management decisions (Lindenmayer and Likens, 2009; Magurran et al., 2010). It is also a key tool for testing and refining models which predict future species distributions and extinctions under different climate change scenarios (Trivedi et al., 2008; Engler et al., 2011). However, reliable botanical recording and monitoring continuity in mountain environments is often limited by remoteness, access, challenging working conditions, time constraints and resource allocation (Sydes, 2008; Stöckli et al., 2011; Mardon and Watts, 2019). There can be very long time intervals of several decades or more between repeat surveys (Grabherr et al., 1994). Research effort generally focuses on inferring population changes from sub-sampling (rather than counting all individuals that occur), presence/absence and species richness data (which does not account for population size), or vegetation surveys of overall community composition (which may overlook rare species) (Lesica and McCune, 2004; Erschbamer et al., 2011; Steinbauer et al., 2018; Porro et al., 2019). Yet monitoring of local population sizes is potentially a more sensitive indicator of future range shifts than larger-scale presence-absence surveys (Cotto et al., 2017). Consequently, there are few complete long-term datasets regularly recording trends in entire arctic-alpine plant populations at mountain outpost sites which encapsulate the emerging threat of climate change.

Here we address this knowledge gap using long-term rare plant monitoring data from the Scottish Highlands in Great Britain. The arctic-alpine flora of Scotland's mountains is of international significance

because it contains populations of climate relicts which are isolated geographically and located at the current low-latitude margins (the rear edge) of their species' distributional ranges (Hampe and Petit, 2005; Sydes, 2008). These populations present an important research system to investigate the demographic trajectories of rare species which will help to inform conservation efforts to preserve regional biodiversity and iconic mountain plants. Our monitoring dataset from the Ben Lawers mountain range in Scotland spans the entire phase of accelerated warming since the early 1990s and contains unusually accurate individual-scale counting of entire sub-populations focusing on species at their geographical low-latitude outposts. By exploring the variation in responses between species and between sub-populations within species, we investigate the following research questions:

1. Are populations of disjunct arctic-alpine plants stable over time and do trends differ between species with contrasting altitudinal ranges?
2. Does altitude influence within species trends between sub-populations i.e., is there any evidence of elevational range shifts or contractions?
3. Are population trends associated with changes in habitat or competitive pressure?

These research questions will further our understanding of how specialist arctic-alpine plants located near maximum local elevations on mountain outpost sites are responding to escalating climate change in contrast to their lower elevation counterparts.

2. Materials and methods

2.1. Study site

This research was conducted on the Ben Lawers mountain range in the Southern Highlands of Scotland (56°30′39″ N, 4°15′45″ W). The site is designated, within different boundaries, as a Site of Special Scientific Interest (SSSI), National Nature Reserve (NNR) and a Special Area of Conservation (SAC). The whole area designated as a SSSI is 5963.33 ha and includes nine mountain summits. The NNR is owned and managed by The National Trust for Scotland (NTS).

The mean annual precipitation from 1970 to 2019 was 2297 mm in the 5x5 km square containing the summit of Ben Lawers (Met Office et al., 2020). Mean annual temperature is 4 °C ranging from a mean monthly minimum of −0.7 °C (February) to a mean monthly maximum of 10.3 °C (July). Ben Lawers reaches 1214 m above sea level, and the underlying geology includes soft Dalradian mica schists giving rise to basic soils. This unusual combination of high altitude and calcareous substrate supports the most important site in Britain for montane plants and arctic-alpine flora (Scott, 2016; Mardon and Watts, 2019).

The primary habitats present at Ben Lawers are all listed in Annex 1 of the European Union Habitat Directives (European Commission, 2013). These include the Priority habitats: Alpine pioneer formations of *Caricion bicoloris-atrofuscae*, Species-rich *Nardus* grasslands and Blanket bogs (Watts, 2020). There is also extensive coverage of Alpine and subalpine calcareous grasslands, Siliceous alpine and boreal grasslands, European dry heaths, Alpine and boreal heaths, Alkaline fen, Sub-Arctic *Salix* spp. scrub, Hydrophilous tall herb fringe community and Calcareous chasmophytic vegetation (Watts, 2014; Watts et al., 2019; Watts, 2020).

2.2. Study species

The perennial vascular plant species featuring in this study (Table 1) had regular and consistent total counts at Ben Lawers during the period 1993–2020 which represent isolated, disjunct mountain outpost populations (Botanical Society of Britain and Ireland, 2022a; GBIF.org, 2022). All have an arctic-montane or boreal-montane global distribution, and a predominantly northern distribution in Europe, with the

Table 1

Arctic-alpine vascular plant species subject to population monitoring analysed here. GB = Great Britain. Distribution information is adapted from the BSBI Atlas 2020 (Stroh et al., In press) and the BSBI Distribution Database (Botanical Society of Britain and Ireland, 2022a). Vegetative height is the mean global trait information extracted from the TRY database (Kattge et al., 2020). Nomenclature follows Stace (2019).

Taxon	Plant type	Family	Vegetative height (cm)	Global distribution	European distribution	Southern European limit in GB	Southern European limit at Ben Lawers	GB Red data book status prior to 2022 (Cheffings et al., 2005)
Carex atrofusca (Lam.) Desv.	Sedge	Cyperaceae	16.7	Circumpolar Arctic-montane	Northern. Restricted distribution in the mountains of Central Europe			Vulnerable
Carex norvegica Jacq.	Sedge	Cyperaceae	15.0	Circumpolar Arctic-montane	Northern. Restricted distribution in the mountains of Central Europe			Least concern
Cystopteris montana Retz.	Fern	Cystopteridaceae	25.5	Circumpolar Boreal-montane	Northern and mountainous regions			Least concern
Erigeron borealis (Vierh.) Simmons	Forb	Asteraceae	12.9	Eurosiberian Arctic-montane	Northern. Replaced by the very similar *Erigeron neglectus* in the Alps	Yes		Vulnerable
Myosotis alpestris F.W. Schmidt	Forb	Boraginaceae	9.5	Circumpolar Arctic-montane	A disjunct distribution across Europe			Near Threatened
Sabulina rubella (Wahlenb.) Hiern	Forb; low-growing cushion former	Caryophyllaceae	4.6	Circumpolar Arctic-montane	Northern. Absent from mountains of Central Europe	Yes	Yes	Vulnerable
Sagina nivalis (Lindblom) Fr.	Forb; low-growing cushion former	Caryophyllaceae	1.8	Circumpolar Arctic-montane	Northern. Absent from mountains of Central Europe	Yes	Yes	Vulnerable[a]
Saxifraga cernua L.	Forb	Saxifragaceae	10.3	Circumpolar Arctic-montane	Northern. Very restricted distribution in the mountains of Central Europe			Vulnerable
Veronica fruticans Schkuhr	Forb	Plantaginaceae	9.4	European Arctic-montane	Northern and mountainous regions; also in Greenland			Near Threatened
Woodsia alpina (Bolton) Gray	Fern	Woodsiaceae	9.3	Circumpolar Boreo-arctic Montane	Northern and mountainous regions			Vulnerable

[a] Updated to Endangered in 2022, see discussion below and the vascular plant Red List compiled by the Botanical Society of Britain and Ireland, 2022b.

exception of *Myosotis alpestris*. *Saxifraga cernua* has a very restricted distribution in the central European mountains. The two cushion-forming members of the Caryophyllaceae (*Sabulina rubella* and *Sagina nivalis*) occur at Ben Lawers at the southern-most limit of their European distribution. The site also holds virtually the entire British population of *S. nivalis* (Mardon and Watts, 2019; Stroh et al., In press). Nomenclature follows Stace (2019).

2.3. Field surveys

Initial surveys of the extent and distribution of the rare arctic-alpine plant species occurring at Ben Lawers were undertaken by the NTS in the early 1980s. Repeat monitoring continued thereafter on a cycle of approximately six years, and involved visiting every known location of a particular species (defined as a discrete "site") and recording the number of plants present. Each site represented a spatially separated population unit, and knowledge of occupied sites was continuously updated and became more accurate as GPS and digital photography technology improved over time. Initially population sizes were estimated, but by the 1990s this method was replaced with full population counts across the whole Ben Lawers range where possible.

Only full population counts are analysed in the research presented here and were carried out using the following methods. At each monitoring site for the species listed in Table 1, accessible plants were marked with a temporary tag as an aid to counting. Searching for small and often inconspicuous arctic-alpines was slow and time-consuming and individuals had the potential to be overlooked. The tags overcame this difficulty by separating the search and find operation from the counting and recording, thus enhancing the accuracy of the results. Tags were typically a "flag" of plastic adhesive tape on a 40 mm zinc-coated panel pin (Fig. 1). Such a marker caused negligible habitat damage and was an optimal size for photographic recording. This survey method follows Mardon and Watts (2019). White plastic garden plant labels were sometimes used to mark taller species such as *Carex atrofusca*.

Plants growing high on cliff ledges or on inaccessible, treacherous terrain were counted by eye using binoculars. For some species it was difficult to determine what constituted a unique individual due to their growth form, particularly when plants were growing close together. In such cases the total number of individual fronds, leaves or flower spikes was used as a proxy for the total number of discrete individuals (Table 2). The location and altitude of each site was recorded using a handheld Garmin eTrex 10 GPS unit with GLONASS. Site photographs

Fig. 1. Temporary flags marking *Sagina nivalis* plants in-situ during a population survey at Ben Lawers (left). A large flowering *S. nivalis* individual of length approximately 45 mm (right). Photographs by Sarah H. Watts.

were taken from the same vantage point where possible, with plant tags in situ to show their distribution (see Fig. 6 as an example). All suitable habitat at each site was fully explored during each re-survey. Any newly colonised locations for our study species were also found by searching areas of suitable habitat beyond the previously recorded sub-populations. These new sites were included in all subsequent population monitoring, as were any extirpated sites at which counts had fallen to zero (to account for any potential recolonisation over time).

Methodological consistency was ensured by long-term continuity of NTS staff, particularly during 2010–2020 when two experienced surveyors carried out most of the fieldwork. All counts of *Erigeron borealis* were made by the same person. Supervision and a robust training in plant identification and survey techniques by D.K. Mardon also maintained the reliability of the 11 other surveyors over the course of the study period.

During the most recent population surveys up to the year 2020, a visual assessment was made of any significant habitat disturbance or change that had taken place at sites where accurate photographic records existed since the 1990s. Site pressures were categorised into the following: landslip, rockfall, trampling by sheep (*Ovis aries*) or "more vegetated" - occurring when the vegetation density and associated plants did not conform to that typically expected for the species being surveyed (Table 2); as described by British plant distribution guides (Preston et al., 2002; Stroh et al., In press) and local observations detailed in internal NTS reports or publications e.g. Mardon and Watts (2019). These pressures were recorded when they affected >50 % of a site's extent; defined as the area occupied by the target species during any survey since the 1990s.

2.4. Data analysis

The first accurate count of the total population size of each species during the 1990s was defined as the baseline population size. The population counts made in subsequent surveys were converted to a percentage of the baseline, to allow for an overall comparison in population trends between species. *S. nivalis* and *S. cernua* counts were adjusted slightly to remove a small number of individual sites which had

not been surveyed consistently each time.

Generalized linear mixed models (GLMMs) were used to determine the effect of time and altitude on the population size of each species incorporating raw counts at the level of the individual survey site. Survey year (i.e. time) and site altitude were included as fixed effects. The GLMMs featured both a random intercept of site and a random intercept of time, to account for the year-to-year variation in counts among sampling years. Short-term population fluctuations were therefore modelled as random effects, giving a more accurate estimate of uncertainty in the long-term trend. The argument for this approach is set out in more detail by Knape (2016) and Daskalova et al. (2021). Random slopes were not included because it was assumed that species counts had a consistent response to time and altitude among each re-survey year and site, and varied only in their overall abundance. The time*altitude interaction was incorporated into the GLMMs to account for differences in population counts between higher elevation and lower elevation sites over time. The interaction was retained in each GLMM if it significantly improved model fit, determined using likelihood ratio tests.

GLMMs were fitted with a negative binomial distribution to correct for over-dispersion, zero-inflation and heteroscedasticity using the glmmTMB package in R Version 4.1.1 (Brooks et al., 2017; R Core Team, 2021). Assessments of model fit, overdispersion, heteroscedasticity and zero inflation were achieved using the DHARMa package (Hartig, 2021). A test of collinearity between fixed effects was undertaken using the variance inflation factor, and both effects were centred and scaled to improve interpretability of the model estimates. Model performance was quantified using the marginal and conditional R^2 (Nakagawa et al., 2017). Population level predictions were fitted for the mean site altitude for each species using the generic predict function in R, and then back-transformed for plotting with the raw data using the exponential function.

The relationship between the maximum altitude of each species at the study site and their population size in the most recent survey relative to the baseline was tested using linear regression. The frequency distribution of site pressures recorded in the most recent survey (landslip, rockfall, "more vegetated" or "no visual pressure") was compared between species using a χ^2 test. Due to a low number of occurrences,

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Table 2

The baseline and most recent population counts for each species during the period 1993–2020, listed in descending order of percentage population change between these surveys. Habitat information is adapted from the BSBI Atlas 2020 (Stroh et al., In press). The trend over time was determined using the generalized linear mixed models (Table 3). Altitude ranges for the Ben Lawers sites are provided, including any instances where the minimum altitude of occupied sites differed between the baseline and most recent survey. GB = Great Britain. *as described in Mardon and Watts (2019) **Myosotis alpestris also occurs on limestone turf in the North Pennines. †These counts have been adjusted to discount a small number of individual sites which had not been surveyed consistently each time; therefore they do not represent the total population size at Ben Lawers. *Cystopteris montana* 2018 total count = 2535. *Saxifraga cernua* 1996 total count = 5335 and 2018 total count = 3142. *Sabulina rubella* 2020 total count = 998. *Sagina nivalis* 1996 total count = 3714 and 2019 total count = 2345.

| Taxon	No. survey sites	Unit of measurement for population size	Typical GB habitat structure	Baseline count (year)	Most recent count (year)	% change	Trend over time	Max. altitude (m asl)	Min. altitude at most recent survey (m asl)	Min. altitude at baseline, if different (m asl)
Cystopteris montana	11	No. of fronds	Sheltered, herbaceous dripping wet rock ledges and gullies with species-rich vegetation	1224 (1993)	2437† (2018)	99 %	Increase	1047	741	
Carex atrofusca	40	No. of flowering spikes	Steep stony flushes among tufts of grasses and relatively closed vegetation	1866 (1993)	3025 (2013)	62 %	Increase	982	756	
Veronica fruticans	63	Individual plants	Herbaceous rock ledges and dry open slopes	913 (1993)	1387 (2016)	52 %	Increase	1055	720	
Carex norvegica	4	No. of flowering spikes	Wet stony slopes and species-rich grassy turf	150 (1993)	191 (2014)	27 %	Stable	968	924	
Woodsia alpina	8	Individual plants	Rock ledges and faces with low-growing herbs	167 (1994)	180 (2012)	8 %	Stable	907	541	
Erigeron borealis	27	Individual plants	Herbaceous rock ledges	560 (1996)	557 (2012)	−0.50 %	Stable	1072	752	
Myosotis alpestris	26	Individual plants	Herbaceous rock ledges and grassy slopes**	9641 (1994)	6525 (2015)	−32 %	Decline	1165	840	
Saxifraga cernua	57	No. of leaves	Sparsely vegetated stony snowbeds, ledges or crevices	5114† (1996)	2337† (2018)	−54 %	Decline	1200	1161	1139
Sabulina rubella	42	Individual plants	Sparsely vegetated dry gravels on boulders, rock ledges or steep slopes	2051 (1997)	852† (2020)	−58 %	Decline	1187	907	905
Sagina nivalis	25	Individual plants (discounting minute seedlings*)	Sparsely vegetated gravels on flushed ground or rock ledges	3514† (1996)	1189† (2019)	−66 %	Decline	1190	915	840
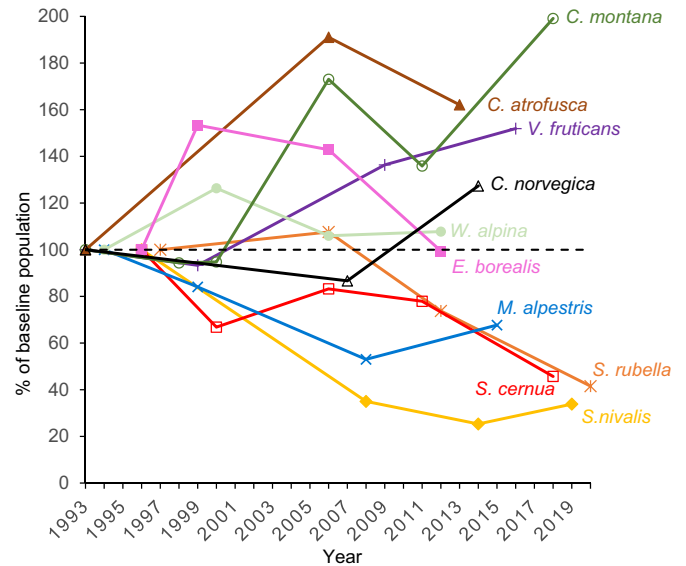
Fig. 2. Changes in the population size of ten arctic-alpine vascular plant species at Ben Lawers in the period 1993–2020, relative to the baseline population present in the 1990s.

landslip and rockfall were combined and records of sheep trampling were removed. *Carex norvegica* was not included in the χ^2 test due to a low number of sites.

3. Results

3.1. Trends in population size over time

There have been contrasting trends in the populations of the ten arctic-alpine vascular plant species surveyed at the study site (Ben Lawers) during the period 1993–2020 (Figs. 2 and 3; Table 2; Appendix). Population monitoring included a total of 88,528 individual plants (or equivalent measurement unit) counted over 27 years across the ten species studied here.

Considering total population counts over the whole study site, three species (*Cystopteris montana*, *Carex atrofusca* and *Veronica fruticans*) have shown population size increases of >50 % at the time of the most recent survey in comparison to the baseline from the early 1990s. Three others have remained relatively unchanged (*Carex norvegica*, *Woodsia alpina* and *Erigeron borealis*). Both groups contain all the ferns and sedges included in the study. The forb *Myosotis alpestris* showed a population decline of 32 % between 1994 and 2015. However, three species (*Saxifraga cernua* and the two cushion formers, *Sabulina rubella* and *Sagina nivalis*) experienced declines of over 50 % of their baseline population size at the end of the survey period.

Concurrently, the negative binomial GLMMs which incorporated counts at the level of the individual survey site (Fig. 3, Table 3) found that survey year (i.e. the progression of time over the study period) had a positive effect on the population size of *C. montana*, *C. atrofusca* and *V. fruticans*, but a negative effect on the population size of *M. alpestris*, *S. cernua*, *S. rubella* and *S. nivalis*.

3.2. The effect of altitude on population trends

Altitude had a negative effect on the site counts of *W. alpina* and *E. borealis,* but a positive effect on the site counts of *M. alpestris*, *S. rubella* and *S. nivalis* (Table 3). An interaction between the fixed effects of time and altitude was also present for five species. For *M. alpestris*, *S. cernua* and *S. nivalis* this interaction was positive, indicating that higher altitude sub-populations of these species did not decline as much over time as lower altitude sub-populations.
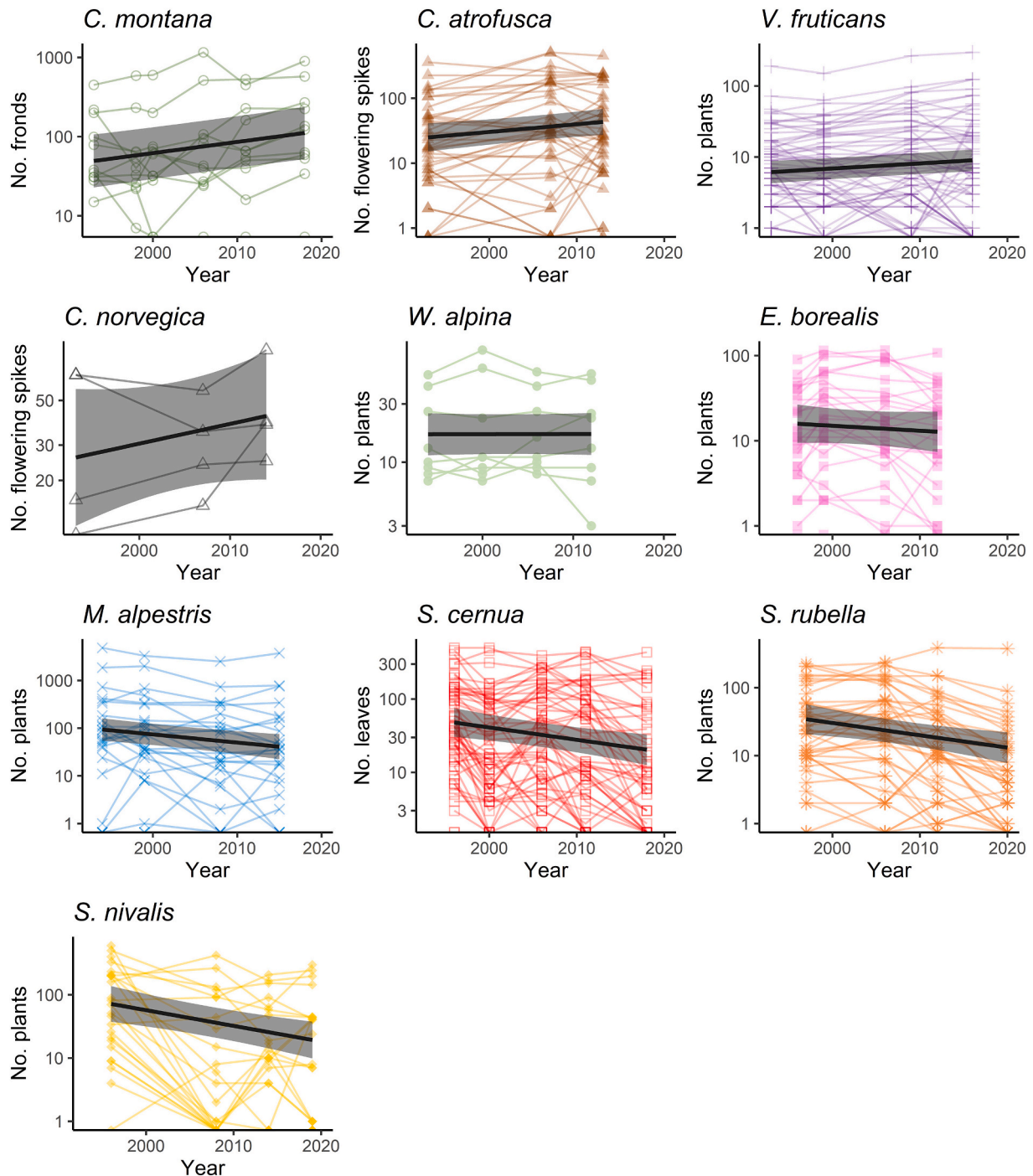
Fig. 3. Raw count data plotted on a logarithmic scale from the surveys of ten arctic-alpine vascular plant species at Ben Lawers in the period 1993–2020. Individual spatially separated survey sites are shown by data points connected with lines. Population level predictions from negative binomial generalized linear mixed models (Table 3) are fitted for the mean site altitude for each species with 95 % Confidence Intervals. Plots using untransformed model predictions are provided in the Appendix.

There was also a significant negative relationship between the maximum altitude of each species at the study site and their population size relative to the baseline ($F(1,8) = 7.98$, $R^2 = 0.50$, $p = 0.022$). The declining species are those occurring at higher elevations with maximum altitudes >1100 m (Fig. 4), which is very close to the summit of the Ben Lawers range at 1214 m. *S. nivalis*, *S. rubella* and *S. cernua* are now exclusively restricted to altitudes above 900 m, after the extirpation of populations in the lowest altitude sites that they previously occupied during the baseline surveys (Table 2).

3.3. Habitat change and competitive pressure

The frequency of site pressures observed during the most recent population surveys was not evenly distributed between species (df = 16, $\chi^2 = 109.94$, $p < 0.001$). Those with the largest population declines relative to the baseline (*S. nivalis*, *S. rubella* and *S. cernua*) had a significantly greater proportion of sites subject to visual changes and disturbance (Fig. 5). All three species grow in a habitat structure of sparse vegetation and gravels, including snowbeds, which contrasts with the typically herbaceous and relatively closed vegetation of the habitats of

Table 3

Negative binomial generalized linear mixed model coefficients (centred and scaled) showing the fixed effects of time and altitude on species counts. The interaction between the fixed effects of time and altitude has been included where it significantly improved model fit, determined using likelihood ratio tests. Numbers in brackets are standard errors (SE) of the model coefficients. Significance levels = *p < 0.05; **p < 0.01; ***p < 0.001.

| Species	Time (SE)	Altitude (SE)	Time × Altitude (SE)	Marginal R²	Conditional R²	No. of sites (n)
C. montana	0.275*** (0.060)	0.025 (0.380)	0.112* (0.049)	0.047	0.833	11
C. atrofusca	0.231** (0.088)	0.228 (0.204)		0.052	0.776	40
V. fruticans	0.147*** (0.031)	−0.040 (0.169)		0.011	0.789	63
C. norvegica	0.206 (0.194)	−0.073 (0.311)		0.078	0.497	4
W. alpina	0.002 (0.050)	−0.569** (0.192)		0.489	0.888	8
E. borealis	−0.084 (0.110)	−0.531* (0.209)	−0.094* (0.042)	0.182	0.858	27
M. alpestris	−0.320** (0.098)	1.124*** (0.241)	0.123* (0.054)	0.422	0.838	26
S. cernua	−0.317*** (0.094)	0.280 (0.170)	0.114* (0.050)	0.079	0.682	57
S. rubella	−0.353** (0.124)	0.537*** (0.156)		0.207	0.676	42
S. nivalis	−0.492*** (0.141)	0.471* (0.236)	0.284** (0.097)	0.198	0.580	25
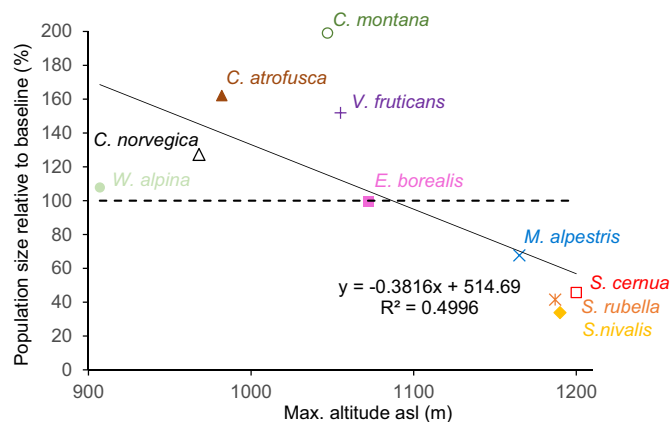
Fig. 4. Population sizes in the most recent survey during the period 1993–2020, expressed as a percentage of the baseline and plotted against the maximum altitude for each species at Ben Lawers.
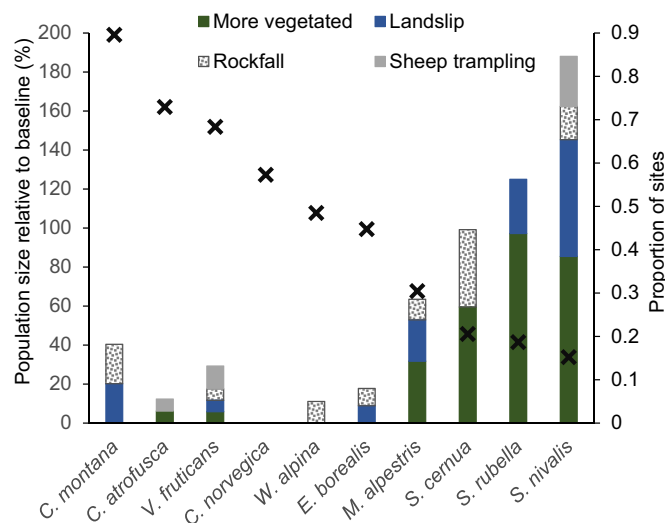

Fig. 5. The proportion of sites that exhibited visual pressures during the most recent survey in the period 1993–2020. These pressures were recorded when they affected >50 % of a site's extent; defined as the area occupied by the target species during any survey since the 1990s. Crosses (X) show the population size in the most recent survey, expressed as a percentage of the baseline.

the stable and increasing species (Table 2). Most notably, 85 % of *S. nivalis* sites had observable pressures across the whole range of categories that were scored, particularly "more vegetated" (38 % of sites; for example see Fig. 6) and landslip (27 %). The species with the highest

proportion of "more vegetated" sites was *S. rubella* (44 %). In contrast, there were no observations of sites being "more vegetated" for *E. borealis*, *W. alpina*, *C. norvegica* and *C. montana*. Rockfall occurred most frequently at *S. cernua* sites (18 %), while sheep trampling only affected a small number of sites of *S. nivalis*, *V. fruticans* and *C. atrofusca*.

4. Discussion

We identify divergent population trends of disjunct mountain plants in the Scottish Highlands monitored in a study spanning from 1993 to 2020. Three arctic-alpine specialists (*Sagina nivalis*, *Sabulina rubella* and *Saxifraga cernua*) have suffered serious declines of over 50 % of their baseline population size. Generalized linear mixed models incorporating individual sub-population counts confirm that these three species have exhibited a negative trend over time. Overall population changes across all species studied were also related to altitude. The arctic-alpine species that have undergone significant declines are those that grow at the highest altitudes across the study site. In contrast, the total population sizes of their lower elevation counterparts remained stable or even increased.

These observations are consistent with predictions of climate warming induced reductions in high elevation floras (Chen et al., 2011; Engler et al., 2011; Niskanen et al., 2019) and align with wider research showing global shifts in community composition on mountain summits and accelerated declines in rear edge plant populations (Lesica and McCune, 2004; Steinbauer et al., 2018; Porro et al., 2019; Rumpf et al., 2019; Lamprecht et al., 2021). Our data indicate that *S. nivalis* and *S. rubella* are at very high risk of extinction at the southern-most limit (the rear edge) of their European distribution. Given that the Ben Lawers range holds virtually the entire British population of *S. nivalis* (Mardon and Watts, 2019), this species should now be considered Endangered in Great Britain, rather than Vulnerable, according to the IUCN Red list criteria A: Population size reduction (IUCN Standards and Petitions Committee, 2022). Indeed, the analyses presented here have led to this change in conservation status being formally recognised for *S. nivalis* in the most recent Vascular Plant Red Data List for Great Britain (Botanical Society of Britain and Ireland, 2022b), demonstrating a direct conservation impact from long-term rare plant monitoring involving individual-scale counting.

By studying trends between sub-populations along local elevational gradients, our work offers a novel insight into the fate of the unique flora at a low-latitude arctic-alpine mountain outpost site. We suggest that other comparable hotspots of regional biodiversity may also be under threat from climate change effects. Although upward migration of species is occurring worldwide, disjunct populations already situated at maximum elevational gradients are faced with "mountaintop extinction" because there is no higher ground available for them to retreat to as temperatures rise (Peters, 1985; Colwell et al., 2008; Lenoir et al., 2008; Reyes-Chávez et al., 2021). Our local observations support this hypothesis since the arctic-alpine species which have experienced

Fig. 6. A visual example of vegetation encroachment by vascular plants occurring at a *Sagina nivalis* site between 2014 (left) and 2019 (right). In 2014 the tagged plants (red) are growing on the dark green moss *Blindia acuta*, a very common associate and key feature of alpine flush habitats (Mardon and Watts, 2019). In 2019 graminoids feature more abundantly across the survey site and the tagged *S. nivalis* plants (blue) are scattered across smaller patches of *B. acuta*. Photographs by Sarah H. Watts.

significant declines have shown more severe losses at their lower altitude sub-population sites in comparison to those nearer the mountain summits. *S. nivalis*, *S. rubella* and *S. cernua* were also extirpated at their lowest altitude locations during our study (Table 2). These results provide evidence for elevational range contractions by the three specialist arctic-alpine plants growing near to maximum local elevations. Uphill distributional shifts and upslope movement of lower altitudinal limits in response to climate change have also been reported for an array of other mountain plant species across alpine, Mediterranean, Andean and subtropical regions (Lenoir et al., 2008; Pauli et al., 2012; Morueta-Holme et al., 2015; Rumpf et al., 2018; Zu et al., 2021).

Our analysis of population trends associated with changes in site pressures demonstrates that the three declining species (*S. nivalis*, *S. rubella* and *S. cernua*) occur in sparsely vegetated, gravelly or snowbed communities which have been subjected to significant habitat disturbance and changes including vegetation encroachment. This finding corroborates observations made by Mardon and Watts (2019) for *S. nivalis* using long-term population monitoring plots involving observations at the individual plant level, and their prediction of similar risks to *S. cernua* and *S. rubella*. Our results can be contextualised by considering broad European trends of thermophilization and biotic homogenization; processes through which rarer, cold adapted specialist species are being displaced by generalists, including common graminoids or more warm-adapted forbs (Smart et al., 2006; Britton et al., 2009; Erschbamer et al., 2011; Gottfried et al., 2012; Ross et al., 2012; Liberati et al., 2019; Porro et al., 2019; Lamprecht et al., 2021).

These new colonisers of mountain summits generally possess more typically lowland traits such as larger sizes and greater specific leaf area (Steinbauer et al., 2018). In contrast, stress tolerant arctic-alpine plants highly adapted to low temperatures are typically small-leaved, low-statured and slow-growing (Körner, 2003). Such traits have particular relevance to cushion formers that colonise bare soil in sparsely vegetated habitats, such as *S. nivalis* and *S. rubella* (Morris and Doak, 1998; Halloy, 2019; Mardon and Watts, 2019). Pioneer species are more vulnerable to competitive exclusion than plants of habitats within closed vegetation (Erschbamer, 2007). Broad shifts in arctic-alpine floras are therefore occurring as a consequence of warming benefiting more vigorous plants, rather than simply because of direct adverse effects of temperature changes on high altitude species (Steinbauer et al., 2018). Accounting for novel competitors will be essential for refining predictions of community interactions in response to climate change (Alexander et al., 2015). Cushion-formers play a key role in arctic-alpine dynamics and local species richness by modifying and stabilising microclimate through soil moisture and nutrient retention, wind protection and heat retention (Cavieres et al., 2002; Cavieres et al., 2007; Gavini et al., 2019). Their displacement will have conservation implications for the high diversity of associated arthropods and localised effects on community productivity (Badano and Cavieres, 2006; Molenda et al., 2012).

Changes in snow cover related to climate change could also explain the high occurrence of vegetation encroachment and disturbance by landslip and rockfall in the habitats of the declining populations of *S. nivalis*, *S. rubella* and *S. cernua*. Trivedi et al. (2007) identified a fall in the number of snow cover days at our study site (Ben Lawers) between

1979 and 2003; particularly at altitudes of 900 m. This finding corroborates broader observations of snow reduction across the British uplands during the last few decades (Watson et al., 1997; Spencer et al., 2014; Brown, 2019; Cameron and Watson, 2019; Rivington et al., 2019; Cameron, 2021; Cameron et al., 2022). Remote sensing has also provided evidence of mountain greening and snow cover declines on a global scale related to climate warming (Chapman, 2013; Hu et al., 2020; Notarnicola, 2020).

Snow plays a vital role in arctic-alpine ecosystem dynamics (Niittynen et al., 2018; Rogora et al., 2018). It moderates surface temperatures, shields plants from frost damage and shelters fragile montane soils from subaerial weathering, freeze-thaw cycles and other erosive processes (Belsky and Moral, 1982; Oke, 1987). Without the protection of a late-lying snowpack, snowbeds and other high-altitude habitats are at increased risk of disturbance from landslip, rockfall and trampling impacts (Huggel et al., 2012; Mardon and Watts, 2019; Chicco et al., 2020). Earlier snow melt will also alter vegetation phenology, lengthen the growing season and further facilitate the invasion of taller, more vigorous species previously restricted to lower elevations (Bannister et al., 2005; Keller et al., 2005; Björk and Molau, 2007; Rammig et al., 2010; Chapman, 2013; Liberati et al., 2019). Additional research is needed to investigate the effects of snow cover reduction on dynamic habitat processes, competitive interactions and plant survival in arctic-alpine habitats, which could be tested experimentally using artificial warming and snow removal (Saavedra et al., 2003; Wipf and Rixen, 2010; Chapman, 2013).

This study also found positive trends over time for three species (*C. montana*, *C. atrofusca* and *V. fruticans*), which had total population increases of over 50 % since the baseline survey in the early 1990s. Three others (*C. norvegica*, *W. alpina* and *E. borealis*) showed no significant variation over time, highlighting that plant species' responses to a changing climate are individualistic (Moen and Lagerström, 2008; O'Sullivan et al., 2020) and can vary between groups with different functional traits (Di Nuzzo et al., 2021; Zu et al., 2021). In contrast to those that have declined, these species are generally taller, associated with herbaceous habitats with a relatively closed canopy cover and do not rely heavily on the availability of bare soil (Tables 1 and 2). They also have a less strongly arctic global distribution and are well established in European mountain ranges to the South of Great Britain. The stable or increasing species are, therefore, not as susceptible to the threats of vegetation encroachment, erosion and declining snow cover than *S. rubella, S. cernua* and *S. nivalis* (Fig. 5), and may even be benefiting from thermophilization. For example, *C. montana, C. atrofusca, C. norvegica* and *W. alpina* are sedges and ferns which grow in sheltered, humid and periodically irrigated sites. Plants of wetter montane vegetation types, such as alpine mires and flushes, are thought to be more resistant to disturbance, biotic homogenization and variations in community composition driven by climate change than drier heaths and upland grasslands (Ross et al., 2012; Ross, 2015; Alatalo et al., 2020).

It is important to acknowledge that other drivers of environmental change and their feedbacks are acting on montane and boreal regions (Wookey et al., 2009). Nitrogen deposition has been linked to variations in community composition through soil acidification and enrichment leading to an invasion of faster growing species such as graminoids (Van Der Wal et al., 2003; Burns, 2004; Stevens et al., 2009; Britton et al., 2019). Nevertheless, Steinbauer et al. (2018) have shown that nitrogen deposition has declined markedly in recent decades and in general does not have a significant effect on accelerated changes in species richness on European mountain summits in comparison to climate warming.

Local disturbance from tourism and changes in grazing management are also recognised threats to arctic-alpine plants in Europe (Thompson and Horsfield, 1997; Monz, 2002; Van Der Wal et al., 2003; Pickering and Hill, 2007; Ross et al., 2012); but our monitoring sites were located away from footpaths on difficult to access terrain, and had a relatively constant density of large herbivores (Mardon and Watts, 2019).

Long-term monitoring continuity will be crucial for accurately following and understanding future trends in the disjunct arctic-alpine plant populations of this study and those at other low-latitude mountain outpost sites. Individual-scale counting of rare species at key locations for regional biodiversity is valuable for informing Red Data lists and national or international conservation status changes due to climate change impacts. Trivedi et al. (2007) predict that snow cover at 1060 m at Ben Lawers will be reduced by 21 % by the 2050s under a low greenhouse gas emissions scenario and by 32 % under a high emissions scenario. There may be no snow at all below 900 m by the 2080s, indicating a bleak long-term outlook for the high-altitude flora at the site (Mardon and Watts, 2019). Continued decline and localised extinctions of *S. nivalis*, *S. rubella* and *S. cernua* is therefore expected in the coming decades. This scenario presents a loss of the cultural and inspirational value that rare species represent, as well as a reduction in regional biodiversity and unique genetic adaptations (Gascon et al., 2015; Hiron et al., 2018). Both in situ and ex situ conservation actions are required to mitigate the impacts of anthropogenic warming at mountain outpost sites before many high altitude arctic-alpine plants become endangered on an international scale (Engler et al., 2011; Porro et al., 2019).

CRediT authorship contribution statement

Sarah H. Watts: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Supervision, Project administration, Funding acquisition. **David K. Mardon**: Conceptualization, Methodology, Investigation, Data Curation, Writing – Review & Editing, Supervision, Project administration, Funding acquisition. **Catherine Mercer**: Formal analysis, Writing – Review & Editing. **Dan Watson**: Methodology, Investigation, Data Curation, Writing – Review & Editing, Supervision, Project administration. **Helen Cole**: Methodology, Investigation, Supervision, Project administration, Funding acquisition. **Rosalind F. Shaw** - Investigation, Writing – Review & Editing. **Alistair S. Jump**: Writing – Review & Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests that could have appeared to influence the work reported in this paper.

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Appendix A

Untransformed population level predictions from negative binomial generalized linear mixed models (Table 3) fitted for the mean site altitude for each species with 95 % Confidence Intervals.
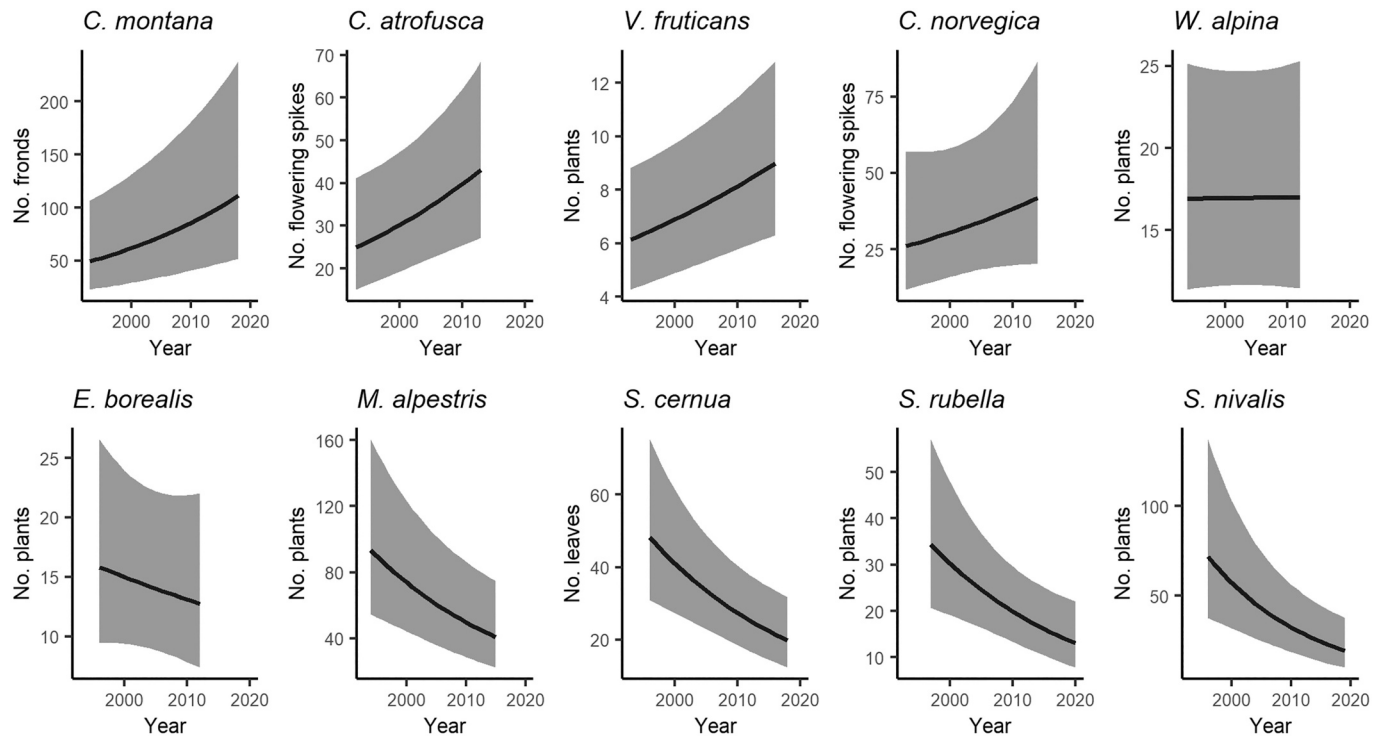
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