

## LETTER

# Arctic and boreal plant species decline at their southern range limits in the Rocky Mountains

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### Abstract

Climate change is predicted to cause a decline in warm-margin plant populations, but this hypothesis has rarely been tested. Understanding which species and habitats are most likely to be affected is critical for adaptive management and conservation. We monitored the density of 46 populations representing 28 species of arctic-alpine or boreal plants at the southern margin of their ranges in the Rocky Mountains of Montana, USA, between 1988 and 2014 and analysed population trends and relationships to phylogeny and habitat. Marginal populations declined overall during the past two decades; however, the mean trend for 18 dicot populations was  $-5.8\%$  per year, but only  $-0.4\%$  per year for the 28 populations of monocots and pteridophytes. Declines in the size of peripheral populations did not differ significantly among tundra, fen and forest habitats. Results of our study support predicted effects of climate change and suggest that vulnerability may depend on phylogeny or associated anatomical/physiological attributes.

### Keywords

arctic-alpine plants, boreal plants, climate change, fens, marginal populations, peripheral populations, range margins, Rocky Mountains.

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## INTRODUCTION

Climate of the earth is changing at an unprecedented rate (Jackson & Overpeck 2000; IPCC 2013) and is predicted to continue (Parmesan & Yohe 2003; IPCC 2013). Understanding and predicting how these changes will affect the distribution and abundance of species has become a major challenge to land managers concerned with conserving biological diversity. The distribution of plants is strongly influenced by climate (Woodward 1987). Palaeontological studies have shown that climate changes have caused shifts in the geographic range of many species and extirpation of many populations in the past (Jackson & Overpeck 2000; Davis & Shaw 2001). As the earth warms, it is natural to assume that the distribution of plants should be declining at their warm latitudinal or altitudinal margins (reviewed in Bakkenes *et al.* 2002; Thomas *et al.* 2004). Several empirical studies support the prediction of upwards altitudinal movement (Peñuelas & Boada 2003; Pauli *et al.* 2007; Beckage *et al.* 2008; Lenoir *et al.* 2008; Parolo & Rossi 2008; Brusca *et al.* 2013; Telwala *et al.* 2013; Lesica 2014). However, far fewer studies have documented latitudinal range shifts in plants. For example, in a meta-analysis of range shifts (Chen *et al.* 2011), 5 of 31 altitudinal range shifts but none of 23 latitudinal range shifts were from plant populations.

There are several possible explanations for lack of evidence for latitudinal range shifts in plants. It may be that climate is less important in determining latitudinal than altitudinal range limits in plants. Range limits are determined by numerous biotic as well as abiotic variables (Chapin *et al.* 1995; Gaston

2009; Sexton *et al.* 2009; Brusca *et al.* 2013), which suggests that in some cases climate does not determine a species' range. Nonetheless, most plant ecologists believe that climate is an important factor determining geographic range limits. Alternatively, there may be more confounding factors with latitude than with altitude at landscape scales. For example, broad-scale, survey-based studies in Sweden and Britain suggest that plant species are declining at their southern margin, but these results are confounded by greater human-caused land-use changes in the south where human populations are greater (Amano *et al.* 2014; Sundberg 2014). Another possibility is that plants are inherently less mobile than animals. For example, responses of plant distributions to habitat fragmentation are much slower in plants than in butterflies (Krauss *et al.* 2010). In this case, we would expect to see plant abundance declining at equatorial range margins, and increasing at polewards margins, even if range shifts are delayed. A final possibility is that plant populations are able to buffer against latitudinal changes in climate. In a 6-year demographic study, Doak & Morris (2010) found little evidence for a decline in two arctic-alpine plant species at the southern limit of their range because decreases in some vital rates were compensated by increases in other vital rates. In this case, we would not expect to see changes in local abundance associated with climate warming, at least not until warming outstripped the capability of plants to buffer the changes.

We know from experimental manipulations that temperature is an important factor determining plant abundance, but that different life forms respond differently to warming, as a result of differences in anatomy and/or physiology. Shrubs

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from arctic Alaska responded positively to 9 years of elevated temperature, but non-vascular plants in the same experiments showed reduced productivity (Chapin *et al.* 1995). Four years of experimental warming in Norwegian alpine tundra resulted in a decline in dwarf shrubs, lichens and mosses due to being outcompeted for light by the coexisting graminoids (Klanderud & Totland 2005). In a meta-analysis of 4-year warming experiments at 13 tundra sites, herbaceous plants responded more strongly to increased temperatures than did shrubs and dwarf shrubs (Arft *et al.* 1999). Another meta-analysis of tundra vegetation found that either shrubs or graminoids increased with warming depending on how cold the sites were (Elmendorf *et al.* 2012).

Responses to warming can also differ depending on the associated plant community. For example, both shrubs and graminoids of Japanese alpine fellfields increased productivity over 7 years of experimental warming, while species from snowbed communities did not (Kudo *et al.* 2010). Artificial warming over 4 years at 13 tundra sites resulted in low arctic sites producing the strongest growth responses, but colder sites demonstrating a greater reproductive response (Arft *et al.* 1999). Several studies have shown that vascular plant responses to warming can be mediated by the associated microbial community (Laua & Lennon 2012; Woodward *et al.* 2012; Worchel *et al.* 2013).

In this study, we analyse trends in abundance over 10–25 years, for 46 populations representing 28 arctic-alpine or boreal plant species at the southern margin of their geographic ranges. Our work was conducted in protected areas in northwestern Montana, where land use has remained stable over the course of the study. Using these data, we evaluate whether these species are declining on average. We also evaluate whether patterns of change in abundance in natural populations are consistent with species- and habitat-specific patterns from warming experiments. Specifically, we used generalised linear mixed models to test the hypotheses that: (1) species are declining at their equatorial range margin. We also test whether (2) rates of declines differed among phylogenetic groups, and (3) rates of decline differed among habitat types. We found that southern peripheral populations have declined significantly, due mainly to the decline in dicotyledonous species; monocots and pteridophytes showed little overall change.

## METHODS

### Study sites

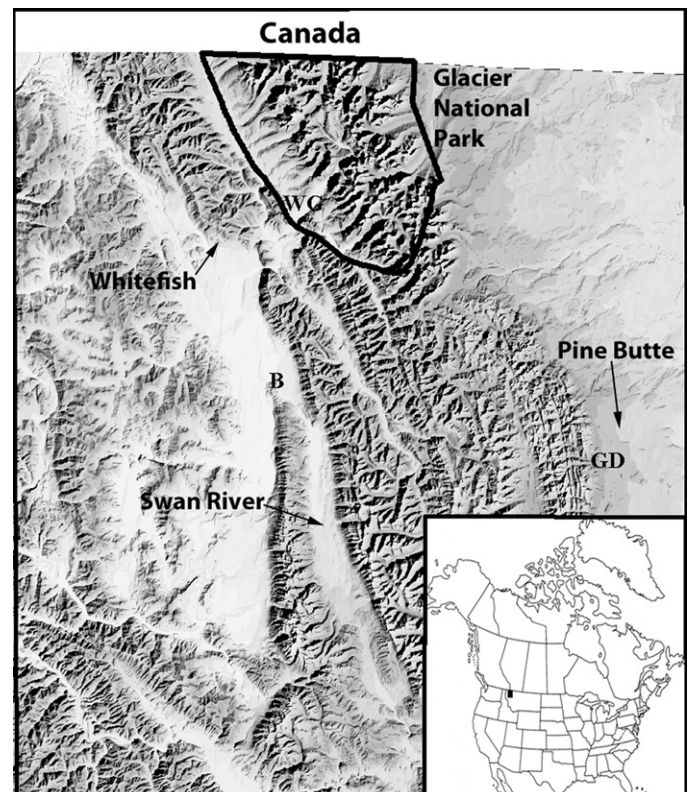
Monitoring was conducted at four study areas in the Northern Rocky Mountains of northwest Montana: (1) Glacier National Park, (2) Pine Butte Swamp Preserve, (3) Swan River Oxbow Preserve and (4) Whitefish Spruce Swamp conservation easement (Fig. 1). All four are natural areas that receive little direct human disturbance. The Glacier National Park study area has 11 study sites separated from each other by at least 4 km of unsuitable habitat. The other three study areas contain only one study site each. Target species occurred in one of three habitats: (1) montane coniferous forests, (2) montane peatlands (i.e. rich or poor fens) and (3) moist alpine tundra receiving moisture from nearby

snowfields. Additional information about the specific study sites is included in Appendix S1.

We chose three weather stations with records that encompass 1950 through 2014 to represent the climate of our study areas. The Gibson Dam station is 30 km southwest of Pine Butte Swamp Preserve at 1390 m elevation. Mean annual precipitation was 43.7 cm. Mean January and July temperatures were  $-5.0^{\circ}\text{C}$  and  $17.1^{\circ}\text{C}$ , respectively. The Bigfork station is 25 km northwest of Swan Oxbow Preserve at 700 m elevation. Mean annual precipitation was 54.0 cm. Mean January and July temperatures were  $-2.3^{\circ}\text{C}$  and  $19.5^{\circ}\text{C}$ , respectively. The West Glacier station is at the west entrance to Glacier National Park at an elevation of 965 m. Mean annual precipitation was 75.3 cm. Mean January and July temperatures were  $-5.4^{\circ}\text{C}$  and  $17.7^{\circ}\text{C}$ , respectively. Whitefish Spruce Swamp is 30 km west of the West Glacier station and 70 km northwest of the Bigfork station. However, climate at the Whitefish site is more similar to the Bigfork site because both are on the margins of Flathead Lake and the Flathead Valley.

### Target species

We monitored abundance of 28 plant species with primarily arctic-alpine or boreal distributions that occur at or near the southern margin of their continuous western North American distribution in northwest Montana over a period of one or



**Figure 1** Location of four study areas in northwest Montana, USA. Locations of the three weather stations, Bigfork (B), Gibson Dam (GD) and West Glacier (WG), are also shown.

two decades (Appendix S2). This monitoring included populations from six separate studies and consequently displays a range of different sampling histories (described in Table S1). Seven species occur in alpine tundra, fourteen in fens, four in forests and one species in both forests and fens. Twenty-two species are herbaceous perennials, two are shrubs and four are annuals. There are 12 monocots, 13 dicots and 3 pteridophytes. Seven of the target species have an arctic-alpine distribution, and 21 are boreal. Eight species are in the Cyperaceae and four are in the Gentianaceae; the remaining 16 species belong to 14 families. We sampled more than 1 population for 11 of the species, for a total of 46 populations of 28 species (see Table S1). Specific information on the target species can be found in Appendix S2. Plant nomenclature follows Lesica (2012).

### Field methods

We collected abundance data for most populations along **subjectively located permanent transects** marked by iron rods driven into the ground. In some instances these were single transects; in others we used sets of parallel transects. For each transect, a fibreglass tape was stretched taut between the endpoints and genets or ramets we counted in sample plots of a size appropriate for that species (Table S1). *Lycopodium lagopus*, *Vaccinium myrtilloides* and one population of *Trichophorum alpinum* were surveyed in temporary sample plots in macroplots defined by GPS coordinates. Canopy cover rather than density was measured for *Gentianella propinqua*. **Sampling was conducted at three separate time periods (1988–1993, 2000–2006 and 2010–2014) that delineate the two decades of the study.** Twenty-two of the 46 populations were sampled during all three sample periods; all were sampled during the latter two sample periods. Thus, **nearly half the populations were followed for two decades and the other half for one decade.** Many species were sampled for three consecutive years in each of the two time periods, whereas others were sampled only once or twice (Table S1).

### Data analysis

**We tested for linear trends in mean annual precipitation and mean summer temperature** at our weather stations between 1950 and 2014 using linear models with fixed effects of site, fixed effects of time and interactions of site and time (i.e. an ANCOVA, with an interaction of the trend through time with the site term). We also tested whether the slope of the trend through time differed among three time periods: 1950–1987 (period prior to our first monitoring), 1988–1999 (our first observation period) and 2000–2014 (our second observation period).

**We analysed trends in plant abundance** using generalised linear mixed models (GLMMs). Only sample plots with at least one plant of a target species recorded in at least 1 year were included in the analyses for that species; other sample plots were assumed to be inappropriate habitat for that species and excluded from analyses. GLMMs were of the general form:

$$E[\ln(N_t)] = \ln(N_0) + \ln(\lambda)t + \varepsilon_t$$

$$\varepsilon_t \sim \text{Normal}[0, \sigma_t]$$

$$N_t \sim \text{Poisson}[\text{mean} = \exp(E[\ln(N_t)])]$$

i.e. overdispersed Poisson family, log-link and regressions of log-transformed abundance through time (see below for a verbal description of the full statistical model, and see Appendix S3 for a full model specification in R and in mathematical equations). In this model, the input data values are  $N_t$ , the number of plants of a particular species in each sample plot in year  $t$ , where  $t$  is the year of data collection. Estimated parameters are population size in year 0,  $N_0$ , which is estimated by the intercept of the GLMM, and the rate of change through time,  $\ln(\lambda)$  which is estimated by the slope of the change in abundance vs. year. For convenience, we set year “0” to be 1990.

This statistical model is equivalent to an “observation error” model of exponential population growth (*sensu* Hilborn & Mangel 1997). We thought most of the variation in our counts was due to observation error for several reasons: (1) plots are samples of a larger population, and individual plants can move in and out of plots through vegetative and seed dispersal; (2) some perennial plants have below-ground life stages (dormant seeds, and “prolonged” growing season dormancy of adult plants; Lesica & Steele 1994); therefore, not all plants are counted in any given year and (3) the count is affected by phenology of the plant populations in relation to the survey time, which is likely to differ among years. Many extensions of this simple model exist, for example, to separate process error and observation error (de Valpine & Hastings 2002; Humbert *et al.* 2009; Holmes *et al.* 2012), but these require time series with more observations than were available for many of our species. Analyses of the longest time series (nine observations over 25 years) indicated that observation error was larger (generally, much larger) than process error in our data (Appendix S4).

Within this general framework, we conducted two sets of analyses to evaluate changes in species abundance through time. Analyses were implemented using the lme4 package (Bates *et al.* 2014) in the open source statistics program, R (R Core Development Team 2013). Fixed effects were evaluated using Type II “marginal” likelihood ratio tests, implemented with the car package (Fox & Weisberg 2011). Random effects were evaluated by comparing AICs (ICtab function, bbmle package; Bolker & R Development Core Team 2014). Within each of the two model sets described below, we first evaluated random effects (where appropriate, see below) against the model with all fixed effects, and then evaluated fixed effects using the selected set of random effects (Zuur *et al.* 2009). Further model specification information is provided in Appendix S3.

First, we analysed data for all species using GLMMs with fixed effects of population (which makes the intercept of the regression line an estimate of initial density for each species at each site), year, year  $\times$  phylogenetic group (separate trends

for dicots vs. non-dicots) and year  $\times$  habitat type (separate trends for populations in fen, forest or tundra), and random effects of year  $\times$  population (i.e. different trends for each population of each species, within its phylogenetic group and habitat type) and initial density in each sample plot (nested within population) modelled as a random effect to account for variation in plant density within sites. We used this model to quantify the overall average change in abundance across all southern range-limit species, and to test whether this trend differed among habitat types and phylogenetic groups. Pteridophytes were pooled with monocots due to the small sample size (3); separating these groups did not improve model fit ( $\chi^2 = 0.1$ ,  $P = 0.789$ ). We also tested whether additional random effects accounting for plant family and species improved model fit; neither did (dAIC = 1.8 and 2.3, for family and species, respectively), and so these effects were not considered further.

Second, we used four of the original studies (Glacier Tundra, Pine Butte, Swan and Whitefish) that had longer time series to test whether trends in abundance differed between the first decade of the study (1988–2006) and the second decade (2000–2014). In addition to fixed effects of “year” and “decade”, this model included fixed effects of phylogeny  $\times$  year and habitat  $\times$  year (as defined in the first model above), as well as phylogeny  $\times$  decade and habitat  $\times$  decade. As in the first analysis, models included an additional fixed effect of “population” to account for initial plant density, and random effects of population  $\times$  year and sampling plot (within population). We repeated this analysis twice with slightly different design matrices to separately estimate (a) the trend and its confidence limits in each decade and (b) the trend in the second decade and the change in trend between the first and second decades (see Appendix S3). These models are equivalent in the sense that one is algebraically convertible into the other, and were used simply to obtain confidence limits for both means and for the difference between them.

## RESULTS

### Climate

There was evidence for climate trends between 1950 and 2014 at all three sites, but the signal differed among sites. Summer temperature showed an overall significant increase over the entire time period from 1950 to 2014 ( $\chi^2 = 9.1$ ,  $P = 0.003$ , d.f. = 1,  $n = 64$  years), with a significant site  $\times$  year interaction ( $\chi^2 = 11.9$ ,  $P = 0.003$ , d.f. = 2). The average rate of temperature increase across sites was  $0.0134 \pm 0.005$  °C per year. When weather stations were analysed separately, summer temperature increased at both West Glacier and Bigfork (representing Swan River and Whitefish), but was stable at Gibson Dam near the Pine Butte site. The temperature trend did not change through time ( $\chi^2 = 0.3$ ,  $P = 0.581$ , d.f. = 1; and  $\chi^2 = 0.0$ ,  $P = 0.880$ , d.f. = 1, for contrasts between the overall trend and the trend from 1988 to 1999 and the trend between 1988–1999 and 2000–2014, respectively).

Precipitation showed an overall significant decrease ( $\chi^2 = 7.3$ ,  $P = 0.007$ , d.f. = 1), and no significant site  $\times$  year

interaction ( $\chi^2 = 1.1$ ,  $P = 0.581$ , d.f. = 2). Overall, the mean trend in precipitation was  $-0.1176 \pm 0.043$  cm per year. The trend in precipitation did not differ among time periods ( $\chi^2 < 1.6$ ,  $P > 0.45$  for both time periods, and for interactions of time period and site).

### Trends in plant abundance

Across all populations, plant abundance declined by a mean of 2.3% per year over the two decades of the study ( $\chi^2 = 11.7$ ,  $P < 0.001$ , Fig. 2). However, there was variation among species and even among populations within the same species (Table 1). Of the 46 populations monitored, 12 were stable (i.e. confidence limits of estimated coefficients for each population included 0), 11 populations increased in plant density (i.e., the lower confidence limit was above 0) and 23 declined (i.e., the upper confidence limit was below 0). Overall the magnitude of declines was greater than the magnitude of increases. Mean trend for populations that increased was +4.1% ramets or genets/plot/year, while the mean trend for declining populations was -6.2%.

Across all populations recorded in both decades, plant density declined in both decades of the study, but the decline was smaller during the second decade ( $\chi^2 = 13.9$ ,  $P < 0.001$ ). The mean decline for these 22 populations recorded during the first decade of the study was -5.3% per year (95% CI -7.4%, -3.1%). The mean decline for these populations during the second decade was -2.7% per year (95% CI -4.9%, -0.5%).

### Effect of phylogeny

Plant density in populations of dicotyledonous species declined more than non-dicots across the 20 years of the study (Table 1, Fig. 2,  $\chi^2 = 14.5$ ,  $P < 0.001$ ). Mean decline across the 18 dicot populations was -5.8% year, while mean decline for the 28 non-dicot populations was -0.4% per year. Of the 18 populations of dicots representing 13 species, 13 populations declined and only 5 increased (2) or were stable (3). The 28 populations of non-dicots included 3 species of pteridophytes and 12 species of monocots. Of these, 10 populations declined and 18 increased (9) or were stable (9). Overall, the average trend was significantly negative for dicots

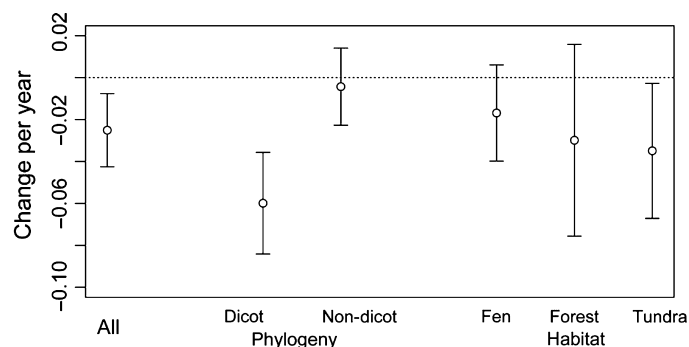


Figure 2 Maximum likelihood estimates of rates of change ( $\ln(\lambda)$ ) from fitted trend models over the full study period,  $\pm 95\%$  confidence intervals, using all data.

**Table 1** Trends (proportional change in genets or ramets) for peripheral populations across both decades (1988–2014) or only one decade (2000–2014) of the study. Arrows following the trends (↑,↓) indicate a statistically significant ( $P < 0.05$ ) increase or decline, respectively

Species	Phylogenetic group	Study	Temporal interval	Trend	SE
<i>Drosera anglica</i>	Dicot	Glacier Fen	2000–2014	0.088 ↑	0.017
<i>Drosera anglica</i>	Dicot	Glacier Fen	2000–2014	−0.013	0.010
<i>Drosera anglica</i>	Dicot	Glacier Fen	2000–2014	0.025 ↑	0.007
<i>Gentianopsis macounii</i>	Dicot	Glacier Fen	2000–2014	0.013	0.012
<i>Gentianopsis macounii</i>	Dicot	Glacier Fen	2000–2014	0.004	0.011
<i>Gentianopsis macounii</i>	Dicot	Pine Butte Fen	1988–2014	−0.119 ↓	0.000
<i>Petasites frigidus</i>	Dicot	Glacier Fen	2000–2014	−0.070 ↓	0.009
<i>Salix serissima</i>	Dicot	Pine Butte Fen	1988–2014	−0.092 ↓	0.002
<i>Utricularia intermedia</i>	Dicot	Glacier Fen	2000–2014	−0.200 ↓	0.010
<i>Halenia deflexa</i>	Dicot	Whitefish	1988–2014	−0.075 ↓	0.000
<i>Vaccinium myrtillus</i>	Dicot	Glacier Rare	2000–2014	−0.035 ↓	0.002
<i>Viola renifolia</i>	Dicot	Whitefish	1988–2014	−0.077 ↓	0.001
<i>Draba macounii</i>	Dicot	Glacier Tundra	1988–2014	−0.100 ↓	0.001
<i>Euphrasia arctica</i>	Dicot	Glacier Tundra	1988–2014	−0.053 ↓	0.000
<i>Gentiana glauca</i>	Dicot	Glacier Tundra	1988–2014	−0.059 ↓	0.000
<i>Gentianella propinqua</i>	Dicot	Glacier Tundra	1988–2014	−0.076 ↓	0.018
<i>Gentianella propinqua</i>	Dicot	Glacier Tundra	1988–2014	−0.095 ↓	0.032
<i>Pinguicula vulgaris</i>	Dicot	Glacier Tundra	1988–2014	−0.007 ↓	0.000
<i>Carex chordorhiza</i>	Monocot	Glacier Fen	2000–2014	−0.008	0.005
<i>Carex livida</i>	Monocot	Glacier Fen	2000–2014	0.021 ↑	0.004
<i>Carex livida</i>	Monocot	Pine Butte Fen	1988–2014	−0.075 ↓	0.001
<i>Carex rostrata</i>	Monocot	Glacier Fen	2000–2014	−0.059 ↓	0.005
<i>Carex tenuiflora</i>	Monocot	Glacier Fen	2000–2014	0.085 ↑	0.007
<i>Cypripedium calceolus</i>	Monocot	Pine Butte Fen	1988–2014	−0.008 ↓	0.000
<i>Dulichium arundinaceum</i>	Monocot	Glacier Fen	2000–2014	−0.028 ↓	0.005
<i>Scheuchzeria palustris</i>	Monocot	Glacier Fen	2000–2014	−0.002	0.004
<i>Scheuchzeria palustris</i>	Monocot	Glacier Fen	2000–2014	0.004	0.005
<i>Scheuchzeria palustris</i>	Monocot	Glacier Fen	2000–2014	0.047 ↑	0.005
<i>Scheuchzeria palustris</i>	Monocot	Glacier Fen	2000–2014	−0.051 ↓	0.004
<i>Trichophorum alpinum</i>	Monocot	Glacier Rare	2000–2014	0.063 ↑	0.005
<i>Trichophorum alpinum</i>	Monocot	Glacier Fen	2000–2014	−0.111 ↓	0.013
<i>Trichophorum cespitosum</i>	Monocot	Glacier Fen	2000–2014	0.003	0.008
<i>Trichophorum cespitosum</i>	Monocot	Glacier Fen	2000–2014	−0.005	0.005
<i>Trichophorum cespitosum</i>	Monocot	Glacier Fen	2000–2014	−0.050	0.031
<i>Trichophorum cespitosum</i>	Monocot	Pine Butte Fen	1988–2014	0.022 ↑	0.000
<i>Cypripedium calceolus</i>	Monocot	Swan	1988–2014	0.001	0.002
<i>Cypripedium calceolus</i>	Monocot	Whitefish	1988–2014	0.000	0.000
<i>Juncus triglumis</i>	Monocot	Glacier Tundra	1988–2014	0.014 ↑	0.001
<i>Juncus triglumis</i>	Monocot	Glacier Tundra	1988–2014	−0.015 ↓	0.003
<i>Kobresia simpliciuscula</i>	Monocot	Glacier Tundra	1988–2014	0.008	0.002
<i>Kobresia simpliciuscula</i>	Monocot	Glacier Tundra	1988–2014	−0.015 ↓	0.000
<i>Tofieldia pusilla</i>	Monocot	Glacier Tundra	1988–2014	−0.009 ↓	0.001
<i>Tofieldia pusilla</i>	Monocot	Glacier Tundra	1988–2014	0.017 ↑	0.001
<i>Dryopteris cristata</i>	Pteridophyte	Whitefish	1988–2014	0.006 ↑	0.000
<i>Lycopodiella inundata</i>	Pteridophyte	Glacier Fen	2000–2014	0.054 ↑	0.003
<i>Lycopodium lagopus</i>	Pteridophyte	Glacier Rare	2000–2014	−0.050 ↓	0.003

(95% CI −8.1%, −3.5%), but not for non-dicots (95% CI −2.2%, +1.4%). Eight species and 16 populations of the non-dicots were in a single family, the Cyperaceae. Our conclusions hold with or without Cyperaceae included in the analysis (phylogeny × trend interaction:  $\chi^2 = 14.1$ ,  $P = 0.0002$  for a reduced data set with Cyperaceae removed; average trend of non-dicots without Cyperaceae was −0.2% decline per year).

Dicotyledonous species declined more than non-dicots in both decades of the study (Fig. 3), but the difference between the two phylogenetic groups was smaller during the second decade ( $\chi^2 = 11.0$ ,  $P < 0.001$ ). In general, the monocots and pteridophytes had similar trends during both periods, whereas

the dicots declined less during the second decade than the first decade. Mean trends for dicots and non-dicots in the first decade were −10.6% (95% CI −12.8%, −8.4%) and −1.0% (95% CI −3.0%, +1.0%) per year, respectively, but −5.8% (95% CI −8.0%, −3.5%) and +0.1% (95% CI −1.9%, +2.0%) per year, respectively, during the second decade.

#### Effect of habitat

Declines in the size of arctic and boreal peripheral populations did not differ among tundra, fen and forest habitats across the two decades of the study (Fig. 2). The mean decline in the 15 species represented by 27 populations found in fens

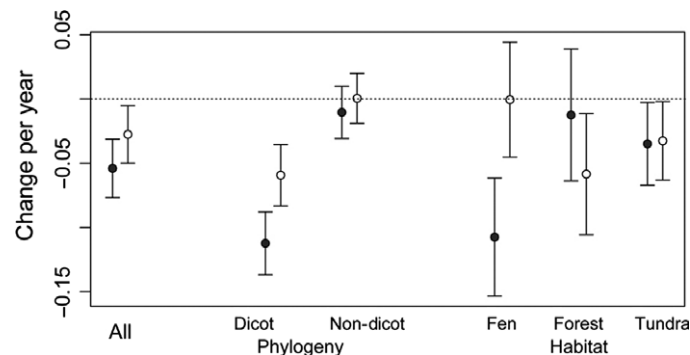
was  $-1.7\%$  per year (95% CI  $-3.9, +0.6$ ). The mean decline in the six populations of five forest species was  $-2.9\%$  per year (95% CI  $-7.3, -1.6$ ). The 13 populations of nine tundra species had a mean decline of  $-3.4\%$  per year (95% CI  $-6.5, +0.3$ ).

## DISCUSSION

We documented a strong overall declining trend for arctic and boreal species at the southern margin of their geographic ranges in the Rocky Mountains concurrent with warming summer temperatures and/or decreasing precipitation. Climate in western Montana over the past two decades has been exceptionally warm (Westerling *et al.* 2006; Pederson *et al.* 2010) with concomitant declines in snowpack (Pederson *et al.* 2011). Growing season temperature has been increasing overall in our region since 1950 at the weather stations representing three of our four study sites. Although mean summer temperature did not increase at Gibson Dam representing the Pine Butte study site, there was a significant decline in annual precipitation, and a decline in snowpack can negatively affect ground water levels that control vegetation patterns in the fen (McAllister 1990). This pattern suggests that ongoing climate change will alter the latitudinal distribution of plant species, at least by contracting their equatorial range limits.

Few other studies have documented latitudinal range contractions in plant populations (Jump *et al.* 2006). Because climate change is recent and ongoing, observational studies similar to ours are needed to refine predictions derived from experiments and/or species distribution models (Guisan & Thuiller 2005; Dawson *et al.* 2011) and to determine whether populations are declining at their equatorial range margins, indicating the possibility of future range contraction.

Although our data support an overall decline in plant populations at their southern range margins, one quarter of the range-limit populations studied increased in abundance. In addition, trends in plant abundance differed between the two decadal periods of our study, but trends in temperature or precipitation did not. One possible explanation for stability of some long-lived, southern range-margin species is the presence



**Figure 3** Maximum likelihood estimates of rates of change ( $\ln(\lambda)$ ) from fitted trend models over the full study period,  $\pm 95\%$  confidence intervals, using populations with data in both time periods. Closed circles (●) are trend estimates between the first two surveys, and open circles (○) are trend estimates between the second and third surveys.

of a lag time between climatic stimuli and demographic responses (Doak & Morris 2010; Dullinger *et al.* 2012; Cronk 2016), leading to an extinction debt, i.e. species that temporarily persist in environments that have become climatically unsuitable. However, declines in abundance of the plant species in our study tended to be slower in the second decade than in the first, which is the opposite pattern one would expect from demographic lags. Monitoring of plant vital rates is needed to rigorously evaluate this hypothesis. In addition, biotic interactions, such as pollination, competition, facilitation or herbivory are likely to be altered as climate changes (Cahill *et al.* 2012). Although these proximate interactions are important in explaining change in abundance for many species, their individualistic nature gives them limited utility in predicting broad-scale response to climate change. Evaluating the role of biotic interactions in explaining our results is beyond the scope of our research but could be a profitable role for future investigations.

Several studies have reported that plant species responded individually to a warming climate (Chapin *et al.* 1995; Dobrowski *et al.* 2011; Elmendorf *et al.* 2012; Brusca *et al.* 2013). Our data suggest that 'individualistic' responses are partly predictable by taking phylogeny into account. Graminoid and non-graminoid monocots may share a warming stress tolerance compared to dicots. Several previous studies have also pointed to a vulnerability of herbaceous dicots to climate warming compared to graminoids. Venn *et al.* (2012) found that graminoids increased compared to broad-leaved species in Australian alpine during the first decade of this century. Forb diversity decreased disproportionately under artificial warming in Alaska tundra (Chapin *et al.* 1995). In a meta-analysis, Walker *et al.* (2006) reported that arctic graminoids increased under experimental warming across the global tundra biome. Common alpine graminoids increased during one of the warmest decades on record in the Austrian Alps (Bahn & Körner 2003). Broad-leaved forbs increased in wet meadows, but declined in drier habitats following a period of drought in the Rocky Mountains (Debinski *et al.* 2010). Similar observations were made on Great Plains grasslands during the great drought of the 1930's. Weaver (1968) reported that drought caused only a shift in the dominance of the grass species, but resulted in the disappearance of many species of forbs (Albertson & Weaver 1944).

Greater resilience to drier conditions by monocots compared to dicots may be the result of anatomical and/or physiological differences. Monocots tend to have fibrous, non-woody, adventitious roots which can be shed under stressful conditions, while perennial dicots often have woody roots that must be supported during periods of drought (Carlquist 2012). Furthermore, an adventitious root-stem junction, typical of monocots, acts as a one-way valve that curtails cavitation, but many dicots are taprooted and prone to suffer embolisms that can extend into the roots and block water movement (Ewers *et al.* 1992). Many monocot stems lack vessels which cavitate more readily than tracheids, so monocots are less prone to embolisms (Carlquist 2012). Monocots are also protected against the effects of detrimental embolisms by having the ability to refill embolised conducting tissues and therefore reestablish the continuity of the water columns

(Dickison 2000). In addition to these anatomical differences, studies suggest that *Kobresia pygmaea*, a graminoid in the Cyperaceae, will increase photosynthetic rate and photosynthetic nitrogen use efficiency under a warming climate (Yang *et al.* 2011), and Yu *et al.* (2015) found that plants with high stoichiometric homeostasis for nitrogen performed better under experimental drought and increased rainfall variability. Physiological traits such as leaf life span, nitrogen concentration and photosynthetic capacity are linked to species distribution across global climate zones, suggesting that they may be important in heat and drought tolerance (Wright *et al.* 2005). More study is needed to determine whether such mechanisms can help explain observations indicating that dicots are generally less drought tolerant than monocots.

It seems reasonable to expect that southern range-margin populations will decline more in some habitats than others with a warming climate. We were surprised by the lack of a significant main effect of habitat in our study. Peripheral fen species did show a lower rate of decline compared to forest or tundra species (Fig. 2), but this difference was not significant. All of our habitats are relatively moist, while interhabitat differences in climate sensitivity are often most pronounced between wet and dry habitats. For example, exposed fellfield plants responded to artificial warming in Japanese alpine sites, but snowbed species did not (Kudo *et al.* 2010). Schöb *et al.* (2009) found a similar result above tree line in the Swiss Alps.

This study is one of the first studies to document declines in plant populations at their southern margins. Results of our study suggest that vulnerability assessment relating to climate change for arctic and boreal species could be improved by incorporating broad phylogenetic groups into climate-based models. Even more useful would be incorporating information on exactly which anatomical/physiological attributes are associated with tolerance to drought and heat stress into vulnerability assessments (Williams *et al.* 2008). Furthermore, **warm-margin populations may themselves be important for conservation** (Hampe & Petit 2005). Although southern range-margin populations can be the most sensitive to a warming climate (Lavergne *et al.* 2005), these same populations may be better adapted to warmer climates than populations farther north. In cases where this is true, southern-margin populations may be an important source for genetic enhancement for more northern and central populations (Bower & Aitken 2008; Sgrò *et al.* 2011).

The uncertainty in projected climate change impacts is one of the greatest challenges facing land managers attempting to address global change. Having the ability to predict species-specific responses to climate change more accurately will help guide land management decisions and prioritise conservation activities (Root & Schneider 2006; Hannah *et al.* 2007; Nuñez *et al.* 2013). Although our data are descriptive, their long-term, unmanipulated nature makes them a valuable addition to warming experiments usually conducted over shorter time spans that reached similar conclusions (Chapin *et al.* 1995; Walker *et al.* 2006). In particular, we caution that not all species will respond equally to changes at their range boundaries, and that we expect equatorial range shifts to occur but to lag behind changes in climate suitability.

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## AUTHORSHIP

PL designed the study and collected the data. EEC analysed the data. PL and EEC wrote the manuscript.

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