LETTER

Demographic compensation and tipping points in climate–induced range shifts

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To persist, species are expected to shift their geographical ranges polewards or to higher elevations as the Earth's climate warms[1–4]. However, although many species' ranges have shifted in historical times, many others have not, or have shifted only at the high-latitude or high-elevation limits, leading to range expansions rather than contractions[5–11]. Given these idiosyncratic responses to climate warming, and their varied implications for species' vulnerability to climate change, a critical task is to understand why some species have not shifted their ranges, particularly at the equatorial or low-elevation limits, and whether such resilience will last as warming continues. Here we show that compensatory changes in demographic rates are buffering southern populations of two North American tundra plants against the negative effects of a warming climate, slowing their northward range shifts, but that this buffering is unlikely to continue indefinitely. Southern populations of both species showed lower survival and recruitment but higher growth of individual plants, possibly owing to longer, warmer growing seasons. Because of these and other compensatory changes, the population growth rates of southern populations are not at present lower than those of northern ones. However, continued warming may yet prove detrimental, as most demographic rates that improved in moderately warmer years declined in the warmest years, with the potential to drive future population declines. Our results emphasize the need for long-term, range-wide measurement of all population processes to detect demographic compensation and to identify nonlinear responses that may lead to sudden range shifts as climatic tipping points are exceeded.

There is overwhelming evidence that many species have shifted their ranges over recent decades[5–11]. The most recent report[12] of the Intergovernmental Panel on Climate Change concluded with "very high confidence" that biological effects of recent warming, including latitudinal and elevational range shifts, are strong. However, these average trends mask considerable variation in responses to warming; in multispecies comparisons of historic and current ranges, typically one-quarter to one-half of the species show no net range shift[6,9,11] (however, also see ref. 13). Moreover, responses to warming frequently differ at the high- versus low-latitude (or elevation) range limits, a pattern observed for butterflies[6], rodents[9] and birds[11]. For example[6], seven species of European butterflies shifted northwards at both their northern and southern range limits, but twice as many species shifted only at the northern boundary, suggesting climate-driven range expansions (another 11 species shifted at neither boundary). If we are to predict the biotic impacts of climate warming better, we must augment the search for historical range shifts with efforts to understand the mechanisms underlying these patterns, so that we can anticipate which species will or will not shift ranges, and which will show net range expansions or contractions due to differential responses at opposite range limits.

Here we report a six-year study of two species of tundra plants across their latitudinal ranges in western North America (Fig. 1), focusing on demographic changes near the southern range limits.

Because they are adapted to life in cold environments, tundra plants are sensitive indicators of biotic responses to climate warming[14,15]. However, individual growth and reproduction of tundra plants may, to a point, improve with increasing temperature[15,16], raising the possibility of compensatory demographic changes. To assess range-wide patterns in demography fully, we quantified the means and year-to-year variances of all vital rates (survival, growth and reproduction) for two species with contrasting morphologies and life histories, the cushion plant *Silene acaulis* (moss campion) and the geophyte *Polygonum viviparum* (alpine bistort, henceforth bistort; see Supplementary Information for more on their biology).
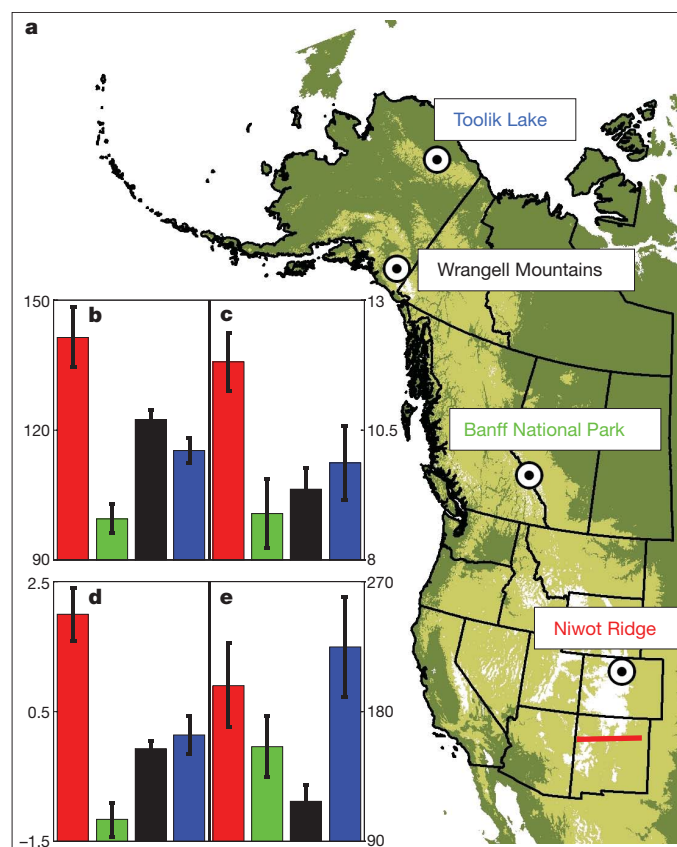

Figure 1 | Locations and climate patterns of field sites. a, Map of field sites. The red line south of Niwot Ridge indicates the southern range limits. Elevations: green, ≤500 m; tan, >500 m and ≤2,000 m; white, >2,000 m. **b**, Mean length (±1 s.e.m.) of the snow-free period in days per year for each region (coloured as in **a**). **c**, Mean July temperature (°C ±1 s.e.m.) for each region. **d**, Mean (±1 s.e.m.) of the first principal component of snow-free period and mean July temperature for each region. **e**, Mean total precipitation (mm ±1 s.e.m.) during the snow-free period for each region. $n = 5$ yr per bar in **b**–**e**.

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As would be predicted if these species were currently undergoing a northward range shift at their southern boundaries, mean annual survival of one or more size classes was lowest in the southernmost populations of both species (Fig. 2; also see Supplementary Fig. 2). All three size classes of moss campion show a pattern of lower survival to the south, with the magnitude of decline being particularly notable for small plants. Models with nonlinear effects also support lower survival of medium-sized bistorts in the southernmost populations (Supplementary Fig. 2). Finally, southernmost populations of both species showed lower average probabilities that a propagule (a seed or bulbil; see Supplementary Methods) would recruit as a newly established individual in subsequent years. For bistorts, this amounted to complete recruitment failure at the lowest latitude in 14 of 20 population–year combinations, and no recruitment in any of these four populations in two of five years.

However, other vital rates showed patterns opposite from expected if conditions in the southern region were so poor as to drive demographic collapse. The growth rate of surviving plants in the southernmost populations always equalled or exceeded that of plants in more northern populations (Fig. 2; also see Supplementary Fig. 2). In particular, growth of small moss campion plants and of bistorts of all sizes was higher on average in the southernmost populations than in any other region. In addition, two reproductive rates (fruits per square centimetre for moss campion and probability of inflorescence production for bistorts) were as high or higher in the southernmost populations than in more northern ones, leading to negative correlations between different performance measures (Fig. 2; also see Supplementary Figs 2 and 3).

To assess the overall effects of these contrasting demographic patterns, we integrated the vital rate estimates for each population into a set of annual projection matrices and used them to compute the long-term stochastic population growth rate[17], λ_s, which incorporates the effects of year-to-year variability in vital rates as well as their means. Although the latitudinal trends in mean rates were most consistent across our study regions, we also found significantly higher temporal variability in several vital rates in the south (Supplementary Figs 4 and 5), which will negatively affect λ_s. However, for neither species did the southernmost populations in our study show the lowest rates of population growth (Fig. 2). For moss campion, λ_s values for the southernmost populations are lower than those for the northernmost populations but higher than those for study populations at intermediate latitudes. For bistorts, there was no difference among regions in the average λ_s values and the average was close to one (that is, a stable population).

Thus, improvements in some aspects of demographic performance in the southern populations, in particular higher individual growth rates, have important population consequences. Because survival increases with size for both species (Fig. 2), higher growth rates more quickly move plants out of the high-mortality size classes, and so offset the population-level effect of lower survival and recruitment rates in the south, thus stabilizing these rear-edge populations[18]. If some vital rates improve with warming temperatures near the range limit, the negative effects on other vital rates of increasing temperatures may be buffered by these improvements[19,20], leading to stable low-latitude or low-elevation range limits even in the face of substantial climatic change[18]. Range limits will remain stable until the joint impact of all worsening vital rates overwhelms the collective effect of all rates that improve, with changes in each rate weighted by its influence on overall population growth.

Relationships between annual vital rates and yearly climate variables argue both that latitudinal differences in climate, particularly temperature, contribute to compensatory patterns in mean vital rates (Fig. 2) and that this compensation will not persist with continued warming. Snow-free period and mean July temperature, both higher on average in the southern region (Fig. 1), encapsulate temperature effects in our study system and are significant predictors of year-to-year variation in
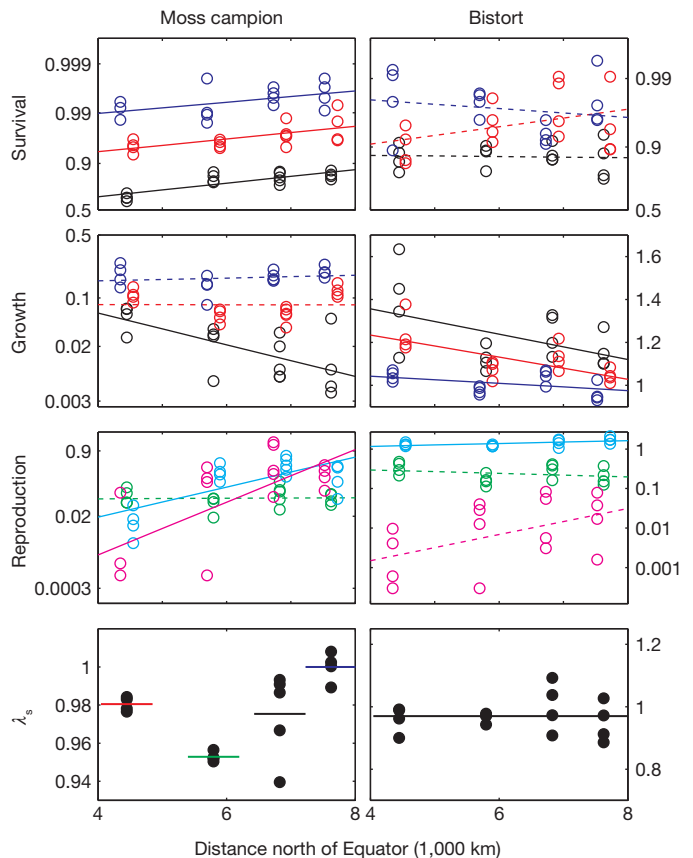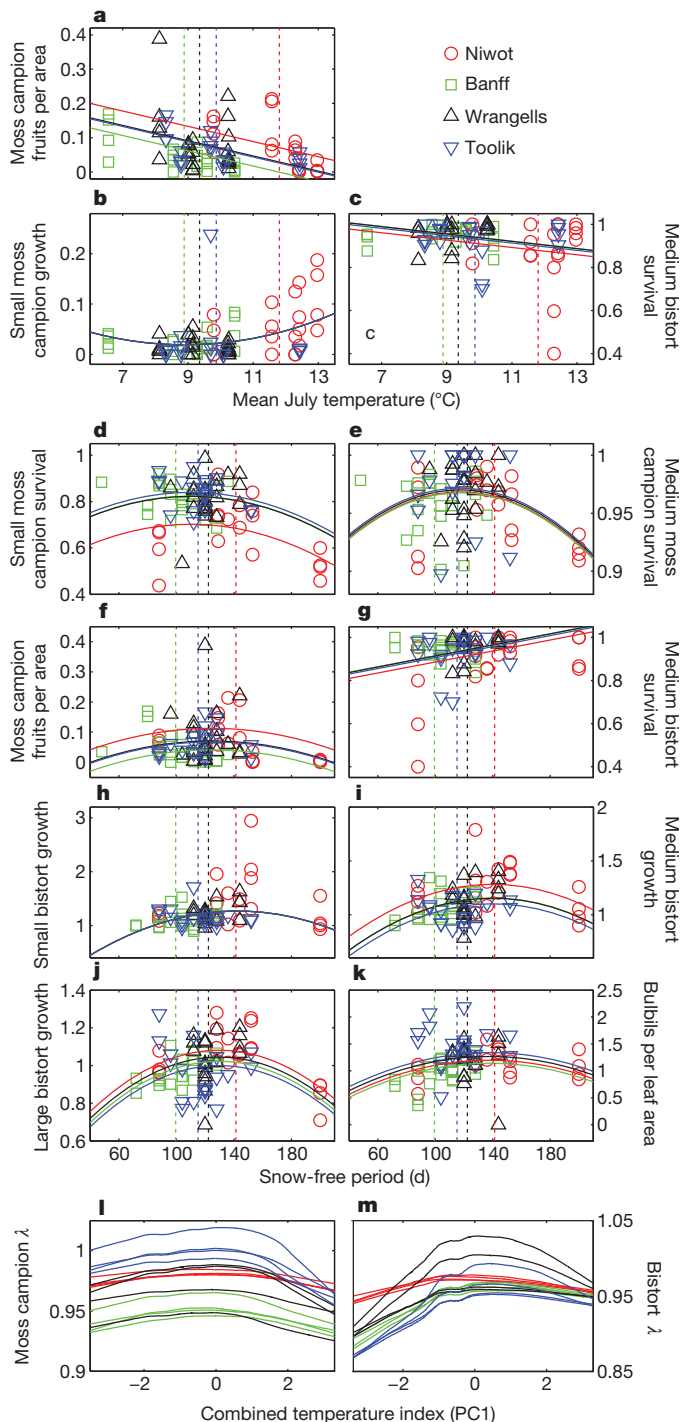

Figure 2 | Mean vital rates and stochastic population growth rates (λ_s) for two tundra plant species along a latitudinal transect. Data points for vital rates are means over six years for each population, with correspondingly coloured lines indicating results of linear regression (regression statistics are in Supplementary Table 2). Each λ_s value is for a different population, with regional means (bars) of the same colour indicating values that do not differ in the most parsimonious model (Supplementary Methods). For survival and growth, small, medium and large plants are black, red and blue, respectively. Moss campion reproductive rates (fecundity and recruitment): green, fruits per square centimetre of cushion; blue and purple, number of seedlings per fruit produced one and two years earlier, respectively. Bistort reproductive rates (fecundity and recruitment): green, probability of producing bulbils; blue, number of bulbils per square root of leaf area; purple, probability that a bulbil recruits as a bulbling one year later. The λ_s values of study populations were computed using Tuljapurkar's approximation[17]. To improve normality, vital rates that represent probabilities were logit-transformed, and moss campion reproductive rates and numbers of bistort bulbils per square root of leaf area were log-transformed. For clarity, some data points are offset slightly in latitude. If there was a significant ($P < 0.05$) latitude effect but no latitude $\times$ size interaction (or, for reproductive rates, latitude $\times$ rate interaction) effect in analysis of covariance (Supplementary Table 1), all regression lines are solid; if the interaction was significant, the regression line is solid only if a separate linear regression showed a significant latitude effect. For bistort, the separate regression of bulbling recruitment probability on latitude was marginally significant ($P = 0.053$; Supplementary Table 2). Additional tests for latitudinal differences were based on model selection results treating region as a categorical variable (Supplementary Methods).

multiple survival, growth and reproductive rates, with effects that accord with the observed latitudinal patterns (Fig. 3). For example, the optimum snow-free periods for survival of small and medium moss campion are respectively 110 and 117 days, lower than the average period (141 days) at the southernmost sites (Fig. 3d, e), where mean survival is also lower (region effects on the survival of small moss campion indicate that other factors are also involved). In contrast, the growth of small moss campion increases with mean July temperature, which also tends to be higher in the south (Fig. 3b). Similarly, bistort growth is highest in the south (Fig. 2), and the

Figure 3 | Effects of two temperature-related variables, mean July temperature and snow-free period, on annual vital rates and on projected population growth rates. a–k, Plots of all vital rates for which the best-supported linear mixed models with a random intercept of region or region and population (Supplementary Table 4) include significant ($P < 0.05$) linear or quadratic regression coefficients for either of the two measures of temperature. Vertical dashed lines show the mean value of the temperature variable in the correspondingly coloured region. For vital rates that are significantly related to both temperature variables, regression lines shown for each variable hold the other variable at its mean value. **l, m**, Simulated rate of population growth (λ) for moss campion (**l**) and bistort (**m**) at different temperatures. Each line shows the fit of a robust locally weighted scatter-plot smoothing (LOWESS) regression model to 1,000 λ values for each study population colour-coded by region. Each λ corresponds to a mean projection matrix built with both temperature-independent and temperature-dependent vital rates, the latter driven by a randomly chosen, but correlated, pair of mean July temperature and snow-free period values. Trends in λ values are plotted against the first principal component of climate, PC1, combining the effects of mean July temperature and snow-free period (Supplementary Methods). Average PC1 is highest in the southern region (Fig. 1d).

This suggests that continued warming can be expected to eventually result in deterioration of most vital rates, potentially shifting a population that is stable owing to contradictory and, hence, compensatory changes at moderate temperatures into rapid decline once a tipping point has been passed (Supplementary Fig. 1). We find support for this possibility in the trends of predicted population growth rates that integrate these varied vital rate responses across temperatures (Fig. 3l, m; also see Supplementary Figs 8 and 9). Simulations predict that both species will have a plateau of high population growth rates across a range of intermediate temperatures, with declines in population performance at both high and low temperatures. These results indicate that the diverse effects of climate on multiple vital rates can jointly result in population stability or even population increase with moderate warming, but that population growth will eventually suffer as all or most vital rates fall with continuing temperature increases (Supplementary Fig. 1).

Both the opposing changes in different vital rates and the nonlinear responses to climate that we have documented for tundra plants are likely to occur in other plant and animal populations[21,22]. Our results caution against using only one or a subset of all life history processes as a basis on which to predict population-level responses and changing geographical ranges in the face of climate change. They also highlight the need for long-term monitoring of all demographic consequences of climate[23], which is a prerequisite for detecting nonlinearities in general and tipping points in particular. With long-term, demographically intensive studies across the geographical ranges of multiple species, we can begin to forecast which species can resist range shifts, which will successfully shift their ranges and which will show rapid declines as a result of continued climate change.

METHODS SUMMARY

From 2001 to 2006, we studied plants in each of 16 bistort and 17 moss campion populations arrayed across four regions: the Niwot Ridge Long-Term Ecological Research Site (Colorado), Banff National Park (Alberta), the Wrangell Mountains (south-central Alaska) and the Toolik Lake Long-Term Ecological Research Site (northern Alaska) (Fig. 1). We began with >300 individually mapped and marked plants in each population. At the end of each growing season, we recorded the survival of pre-existing plants, the size and reproductive output of survivors, and the appearance of new recruits, which we then followed in subsequent years. Altogether, our study included 35,386 individual plant-years for moss campion and 23,980 for bistort. For each species, we computed nine vital rates, including annual survival and growth rates for three size classes and three components of reproduction (including both fecundity and recruitment rates). For moss campion, reproductive rates are the number of fruits per square centimetre of plant surface area and the number of seedlings emerging per fruit produced one and two years earlier; for bistort, reproductive rates are the probability of producing bulbils (asexual propagules that are the only means of reproduction in our populations), the number of bulbils per square root of leaf area and the fraction of bulbils

optimal snow-free periods for the growth of small, medium and large bistorts—143, 140 and 130 days, respectively (Fig. 3h–j)—are all close to the average in the southern region. Compensating for this trend, the survival of medium bistort declines with both latitude and mean July temperature (Fig. 3c). Although other ecological and climatic factors apart from temperature (Supplementary Methods) may also contribute to latitudinal trends in vital rates, the regional differences we see are not consistent with latitudinal patterns in precipitation or intraspecific competition (Fig. 1e; also see Supplementary Fig. 7).

A striking feature of the relationships between vital rates and temperature-related climate variables (Fig. 3) is that with warming from low to moderate temperatures most vital rates increase; across moderate temperatures some rates increase, some are stable and some decrease; and from moderate to high temperatures most rates decrease.

recruiting as small plants ('bulblings') the following year. We tested for both linear and nonlinear trends in vital rates and population growth rates with latitude. We also fitted mixed models of yearly vital rates against two measures of growing-season temperature, including random region and population effects, and then used the best-supported models to simulate population growth rates across a range of temperature conditions.

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